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GENETIC RESPONSE OF JACK PINE SEEDLING TO NUTRIENT AND WATER TREATMENTS: IMPLICATIONS FOR EARLY GENETIC EVALUATION

BY

PENGXIN LU ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE

DEPARTMENT OF FOREST SCIENCE

EDMONTON, ALBERTA

SPRING, 1995

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Abstract

Reliable prediction of mature performance with early (juvenile) traits can substantially shorten the breeding cycle in long-aged tree breeding program. There are two prerequisites for making early selection successful: heritable early traits and high juvenile-mature correlation. Previous early tests have suggested that the early testing environments in which progenies are evaluated could greatly affect juvenile-mature correlation. In this study, 25 open-pollinated jack pine families with known field performance were tested in the greenhouse under two levels of nutrient and three levels of water conditions to investigate: *i*) the effects of nutrient and water treatments on the growth performance of first-year jack pine seedlings, *ii*) the genetic response among open-pollinated jack pine families to the nutrient and water treatments and the degree of family-by-treatment (G x E) interactions, and *iii*) the genetic correlation among juvenile traits and family correlation between juvenile traits and 15-year field tree height under the early-testing nutrient and water conditions.

Results indicated that low nutrient concentration (20 ppm) in the soil severely retarded seedling size, reduced seedling growth period and increased the root/shoot ratio in dry biomass allocation. The effect of water treatment was not significant for seedling height growth but was significant for seedling basal diameter and biomass growth. Nutrient by water treatment interaction was negligible for most seedling traits.

Genetic variation among the 25 open-pollinated jack pine families was highly significant for all early traits assessed. High family heritability (0.8-0.9) was estimated for absolute height growth and height increments of seedling, indicating their strong genetic control. Despite the tendency that fast-growing families showed greater response to environmental changes, family performance was fairly stable both in seedlings in the greenhouse and in adult trees in the field as indicated by their G x E interactions.

Moderate to strong correlations were obtained between 20 different seedling traits and 15-year field growth, which indicated the possibility of making selections at the seedling stage in jack pine. Several seedling traits, including seedling height, height increment and seedling organ dry biomass yielded satisfactory type B genetic correlations (0.57-0.71) and Spearman family rank correlation (0.6-0.74). The percentage of correct identification of 15-year field family classes with 20 different seedling traits averaged 55% for the fast- and slow-growing field family classes and 43% for the average-growing field family class. The percentage of serious mis-identification of field family classes was under 8% for all seedling traits.

Low nutrient conditions, especially the treatment combination of low nutrient and frequent watering in the greenhouse, gave persistently better correlation or prediction with 15-year field growth. Despite the possible cause of sampling error, it was suspected that mimicking field nutrient conditions would improve early testing results in jack pine in Saskatchewan.

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CHAPTER 1 RESPONSE OF FIRST-YEAR JACK PINE SEEDLINGS TO NUTRIENT AND WATER TREATMENTS

1.1 Introduction

Early selection of forest trees relies on high genetic correlations between juvenile and mature traits and high heritability of juvenile traits (Lambeth 1980, Jiang 1987). However, in several extensive studies of important tree species, early test results have been inconclusive and sometimes conflicting (Lascoux et al. 1992; Eriksson et al. 1993). Among several possible reasons that might account for the controversial results, early test environment was suspected as a major contributing factor in weakening the age-age correlations (Cannell et al. 1978; Li et al. 1991). Therefore, the identification of the optimum early test environment has received increasing attention in recent years.

Within a given breeding zone, soil nutrient and moisture conditions are usually the most variable field factors affecting the growth and development of forest trees. Genotype-by-environment (GE) interactions have been reported among sites and treatments differing in nutrient or water availabilities (Pritchett and Goddard 1967; Jahromi et al. 1976; Owino 1977; La Farge and Kraus 1981; Johnson and Burdon 1990; Pederick 1990; Wu 1993). Forest tree seedlings in the nursery or greenhouse have also exhibited strong response to water and nutrient cultural regimes. For instance, Li et al.(1991) found significant differences among open-pollinated loblolly pine (*Pinus taeda* L.) families in nitrogen use efficiency

(NUE). Smith et al. (1992) reported significant family and family-by-nitrogen interaction on first-year seedling shoot growth traits in 64 open-pollinated slash pine (*Pinus elliottii* Engelm.) families growing under two nitrogen levels. Cannell et al. (1978) observed significant growth differences and family-by-water treatment interaction among 16 open-pollinated loblolly pine families growing under different water stresses. Waxler and van Buijtenen (1981) found significant family-by-water treatment interaction for 10 known fast- and slow-growing open-pollinated loblolly pine families. It appears to be a common tendency rather than an exception that GE interaction occurs in early tests in the greenhouse and in field plantations.

Previous early tests have suggested an important role that GE interaction might play in weakening the age-age correlations. For instance, in an early test of loblolly pine, Cannell et al. (1978) found family mean correlations between nursery performance and field volume of 8-year loblolly pine were highest when the water conditions in the nursery resemble those in the field. This observation was based on the fact that growth rate of well-watered seedlings in the nursery was correlated significantly with the stem volume at poorly drained sites and not on well-drained sites. In addition, growth rate of mildly water-stressed seedlings was correlated significantly with stem volume at well-drained sites and not on poorly drained sites. Feret (1982) confirmed that family correlations between plantation height and seedling growth under stress were plantation specific in 40 open-pollinated ponderosa pine *(Pinus Ponderosa* Dougl. ex Laws) families under different water stress conditions. Li et al. (1991) obtained higher early-mature correlations with 23 open-pollinated loblolly pine families under low nitrogen level and believed this was the result of mimicking field nitrogen deficient conditions. In an early test of lodgepole pine (*Pinus contorta* spp. *latifolia* Engelm.), Wu (1993) grew 110 open-pollinated families in the greenhouse under optimal water and nutrient conditions for two growing seasons. Most genetic correlations between seedling traits and 9-year tree height in the field were found significant (24 seedling traits) only on one of the four sites with the highest site quality. In jack pine (*Pinus banksiana* Lamb.) and maritime pine (*Pinus pinaster* Ait.), favourable or growth-accelerating conditions yielded high age-age correlations (Carter et al. 1990; Riemenscheider 1988; Magnussen and Yeatman 1986; Lascoux et al. 1992). However, considering the abundance of rainfall and good soil conditions in the northeastern U.S. and eastern Canada where jack pine plantations were established, it is uncertain if the results are applicable to prairie provinces where jack pines often grow on sandy soil and where drought spells are frequent.

If GE interaction is a major contributor to the weak age-age correlations, testing genotypes under different water and nutrient conditions might be an effective way to identify the optimum early testing environment for predicting the performance of trees growing under different field conditions. Except for a limited number of studies that studied genetic variation and age-age correlations under a single treatment of nutrient or water, few studies considered the joint effect of water and nutrient. There is no known genetic study of both nutrient and watering regimes in jack pine. In this study, I tested the hypothesis that different early testing environments produce considerably different early test results. My specific objective was to study the genetic response among open-pollinated jack pine families to water and nutrient treatments.

1.2 Materials and method

1.2.1 Materials

Twenty five open-pollinated jack pine families used in this study were chosen from the 216 families that are being field tested on four sites in the Western Breeding District in Saskatchewan. Of the 25 families, 8 were randomly drawn from the fast-growing class (family ranking 1 to 19), 9 were taken from the average-growing class (family ranking 98 to 117) and the remaining 8 were from the slow-growing class (family ranking from 197 to 216). Families were classified according to their average 15-year height across sites.

Before sowing, three independent samples of 100 seeds were drawn from each of the families for estimation of the family mean seed weight. Seedlings were grown in the greenhouse, University of Alberta, under natural photoperiod (about 16-17 hours/day) and controlled temperature of 20-25°C. The pots used throughout the experiment were of size 2.5 x 2.0 x 9.0" (703 cm^3 in volume), which were filled with 1:1:1 mixture of peat moss, vermiculite and sterile sand.

Seeds were directly sown into pots during the period May 17-19, 1993, with 3 seeds per family in each pot. Every pot had 2-3 germinates in two weeks. Immediately after germination, fungicide was applied according to instruction to prevent seedling damping off, and seedlings were randomly thinned to one plant per pot. For the first two weeks after sowing, deionized water was supplied daily to maintain soil moist. Subsequent watering was reduced to twice a week. Water pH value was adjusted with 1% sulphuric acid to about 5.8 throughout the study period. Starting on June 14, a solution of complete fertilizer 20-20-20 (200 ppm) was supplied at two-week interval in conjunction with seedling watering. Prior to each fertilization, seedlings were flushed with deionized water to prevent the build up of salt, then fertilizer solution was applied to ensure stable and even nutrient concentration in the soil.

Nutrient and water treatments started on July 27 when seedlings were about 8 weeks old. The experimental design was a 10 x 3 x 2 x 25 randomized complete block split-plot design, representing 10 block (replications), 3 levels of water treatment, 2 levels of fertilizer treatment and 25 families belonging to 3 field family classes. The 3 levels of water treatment, watering twice a week (W3), once a week (W2) and once every two weeks (W1), were chosen because under greenhouse conditions, a watering interval of 3 days, 7 days and more than 10 days could result in optimal, mild water stress and severe water stress, respectively, to seedlings (Van Den Driessche 1991, Wu 1993). We did not sample seedling tissue to measure internal water status during the growing season for fear of damage to the seedlings. However, in a pilot study, we found that watering at a 2-week interval did not cause severe injury or death to the seedlings.

Nutrient treatment consisted of 200 ppm and 20 ppm solutions of complete fertilizer 20-20-20 (plus 1.7 ppm iron chelate) applying to seedlings at an interval of two weeks. The choice of fertilizer and concentrations were based on Scarratt (1987), Giertych and Farrar (1962) and Carter at al. (1990), who suggested 20-20-20 general purpose fertilizer at a concentration of 200 ppm was effective in producing well-balanced, vigorous seedlings. The 20 ppm concentration was used to simulate nutrient deficient conditions.

There were 6 main plots (trays) within each block, to which the 3 levels of water and 2 levels of nutrient treatments were applied. Each main plot contained 25 seedling pots, and the 25 families belonging to the 3 field family classes were randomly allocated within each of the main plot as 1-plant subplot. The original number of pots in the experiment was 1500, with 60 pots per family, 750 pots per fertilizer treatment level, 500 pots per water treatment level and 150 pots per block (replication). However, the data for statistical analyses were unbalanced due to occasional death of some seedlings (about 5%).

On October 8, 1993, artificial high pressure sodium vapour light (with average photosynthetically active radiation intensity of 111 umol.m^{-2}.s^{-1}) was supplemented at 17 hours/day to promote seedling diameter and biomass growth (at this time, 99% of the seedlings formed apical terminal buds). This condition was kept until the end of the experiment on January 6, 1994.

1.2.2 Measurements

There were three reasons why the observations of seedling growth in the greenhouse were focused on morphological traits. First, morphological traits, such as stem height growth, stem dry weight, or shoot/root ratio etc., were among the most promising traits in predicting mature field performance (Cannell et al. 1978; Smith et al. 1992; Greenwood and Volkaert 1991). Second, morphological traits could be measured on a large number of seedlings in a short time. Measurement errors of quantitative traits were smaller relative to physiological traits because the latter were often associated with sample size restriction and variation in measuring environments, time and plant growing status. Third, morphological traits were the cheapest characteristics of plant to be measured.

Seedling height and basal diameter was measured at: (1) two months (immediately before treatments began, H1); (2) four months (H2 and D1); (3) five months (H3 and D2); and (4) six months (before final harvest, H4 and D3). Stem length between soil surface and the first leaf (H0) was also measured at two months. Seedling heights were measured as the length between soil surface to the point of apical meristem except H1 which was measured from soil surface to the top of leaves.

Between August 18 and October 6, the date of seedling apical terminal bud formation was observed weekly to determine the response of families to the shortening day-time. The presence of terminal bud was determined by cessation of apical growth and visible white terminal bud. The length of growing period (LGP) was calculated from June 1, 1993 to the date of terminal bud formation.

Seedlings were individually harvested in January, 1994. A whole plant was separated into parts of needle (Ne), branches (Br), upper stem (stem with needles and branches, Ust), lower stem (stem alone, Lst) and roots (Rt). Plant roots were carefully washed of soil with tap water. All tissue parts were oven dried at 80 °C for 48 hours and their dry weights were measured. Shoot dry biomass (SB) was calculated as the sum of Ne, Br, Ust and Lst, while total biomass was determined as the sum of SB and Rt.

Several traits were derived from the above observations. They were: net height growth increments NH1-0 (i.e. H1-H0), NH2-0 (i.e. H2-H0), NH3-0 (i.e. H3-H0), NH4-0 (i.e. H4-H0), NH3-2 (i.e. H3-H2), NH4-2 (i.e. H4-H2) and NH4-3 (i.e. H4-H3); net diameter growth increments ND2-1 (i.e. D2-D1), ND3-1 (i.e. D3-D1) and ND3-2 (i.e. D3-D2); and ratio traits such as H/D (the ratio of height growth to diameter growth i.e. H4/D3) and S/R (the ratio of shoot dry biomass to root dry biomass i.e. SB/Rt). The two ratio traits have been reported to be of significance in determining plant biomass allocation, growth potential and adaptability (Cannell 1978; Li et al. 1991; Wu 1993).

1.2.3 Methods of statistical analyses

Analyses of variance (ANOVA) were conducted to detect the effects of nutrient and water treatments on jack pine seedling growth. SAS procedure GLM (SAS Institute Inc. 1985) was performed with a mixed linear model for all traits:

$$Y_{ijklm} = u + B_i + N_j + W_k + BN_{ij} + BW_{ik} + NW_{jk} + BNW_{ijk} + C_l + F_{m(l)} + NC_{jl} + NF_{jm(l)} + WC_{kl} + WF_{km(l)} + NWC_{jkl} + NWF_{jkm(l)} + E_{ijklm} \quad (1.1)$$

where

Y_{ijklm} = the observation of the *m*th family within the *l*th field family class under the treatment of *j*th nutrient level and *k*th water level in the *i*th block;

u = overall experimental mean,

B_i = replication effect (random),

N_j = nutrient effect (fixed),

W_k = water effect (fixed),

BN_{ij} = effect of block by nutrient interaction (random),

BW_{ik} = effect of block by water interaction (random),

NW_{jk} = effect of nutrient by water interaction (fixed),

BNW_{ijk} = effect of block by nutrient by water interaction (random),

C_l = effect of field family growing class (fixed),

$F_{m(l)}$= effect of family within class (random),

NC_{jl} = effect of nutrient by family class interaction (fixed),

$NF_{jm(l)}$=effect of nutrient by family within class interaction (random),

WC_{kl} = effect of water by family class interaction (fixed),

$WF_{km(l)}$= effect of water by family within class interaction (random),

NWC_{jkl}=effect of nutrient by water by family class interaction(fixed),

$NWF_{jkm(l)}$=effect of nutrient by water by family within family class interaction (random),

E_{ijklm} = residual error.

Seedling height (H1) measured before the treatment was used as a co-variable to adjust for the effects of initial seedling size differences on the treatment effect. Due to data imbalance, only adjusted (type III) mean squares were used in all F-tests. When appropriate error terms were not directly available, Satterthwaite (1946) approximation method was used. Differences among means of treatment levels were tested with the method of T-test.

Effects of seed weight on seedling growth were examined with a simple regression model on family mean basis in each nutrient and water treatments and their combinations. The homogeneity of regression parameters between any two different treatment levels was tested for each growth trait using the model:

$$Y_{ij}=b_0 + b_{0i} + b_1Sdwt_j + b_{1i}Sdwt_j + e_{ij} \quad (i=1, 2; \text{ and } j=1, 2, ..., 25) \quad (1.2)$$

where Y_{ij} is the *j*th family mean value for seedling growth trait in the *i*th treatment (or treatment combination) level, $Sdwt_j$ is the *j*th mean family seed weight, b_0 and b_1 are the intercept and slope respectively in a simple regression model using data from treatment level 1 only, b_{0i} and b_{1i} are additional intercept and slope created by adding data from treatment level 2 into the model, e_{ij} is the error term of regression. A significant b_{0i} indicates different seed weight effects between the two treatment levels in the intercept of regression, and a significant b_{1i} indicates the different seed weight effects between the two treatment levels in the slope of the regression. Non-significant b_{0i} and b_{1i} will indicate that the data from treatment level 1 and level 2 can be combined to estimate regression parameters jointly. Seed weight adjustment was conducted following the approach of St. Clair and Adams (1991).

To observe the effects of treatments on genetic variance component estimates, separate ANOVAs were subsequently preformed under individual nutrient or water treatment level or their combinations. For traits with significant seed weight effect, genetic variance components were estimated before and after seed weight adjustment to obtain information on the degree to which genetic variations might be exaggerated by seed weight differences. The ANOVA models used for individual nutrient level, water level and each combination of nutrient and water level were respectively:

$$Y_{iklm} = u_j + B_i + W_k + BW_{ik} + C_l + WC_{kl} + F(C)_{m(l)} + WF(C)_{km(l)} + E_{iklm} \tag{1.3}$$

$$Y_{ijlm} = u_k + B_i + N_j + BN_{ij} + C_l + NC_{jl} + F(C)_{m(l)} + NF(C)_{jm(l)} + E_{ijlm} \quad (1.4)$$

$$Y_{ilm} = u_{ij} + B_i + C_l + F(c)_{m(l)} + E_{ilm} \quad (1.5)$$

where the Y, u, B, N, W, C, F, E, i, j, k, l, and m have the same definitions as in formula (1.1).

Under the assumption that open-pollinated families estimate one fourth of the additive genetic variance (Yeh and Rasmussen 1985), family (within classes) and individual heritability were estimated as:

$$h^2_{f/c} = \frac{\sigma^2_{m(l)}}{\sigma^2_{m(l)} + \frac{k_2\sigma^2_{m(l)\cdot j}}{k_1} + \frac{k_3\sigma^2_{m(l)\cdot k}}{k_1} + \frac{k_4\sigma^2_{m(l)\cdot j\cdot k}}{k_1} + \frac{\sigma^2_e}{k_1}} \quad (1.6)$$

$$h^2_i = \frac{4\sigma^2_{m(l)}}{\sigma^2_{m(l)} + \sigma^2_{m(l)\cdot j} + \sigma^2_{m(l)\cdot k} + \sigma^2_{m(l)\cdot j\cdot k} + \sigma^2_e} \quad (1.7)$$

Variance components were partitioned in accordance with the expected mean square appropriate. The approximate standard errors of heritability estimates were obtained using the formula given by Nyquist (1991) .

Type B genetic correlation, which measures the association between individuals belonging to the same genetic group but growing in different environments, were calculated for the same seedling trait measured in two testing treatment levels following the method of Yamada (1962). Family stabilities across treatments were evaluated with methods of joint regression analysis (Freeman 1973), type B genetic correlation and Spearman family rank correlation.

Genetic correlations (r_g) and phenotypic correlations (r_p) between any two seedling traits measured on the same plants were estimated following Falconer (1981):

$$r_g = \frac{cov_f(1,2)}{\sqrt{\sigma^2_{f1}\sigma^2_{f2}}} \tag{1.8}$$

$$r_p = \frac{cov_p(1,2)}{\sqrt{\sigma^2_{p1}\sigma^2_{p2}}} \tag{1.9}$$

where $cov_f(1,2)$ and $cov_p(1,2)$ are genetic and phenotypic covariances between traits; σ_{f1}^2, σ_{f2}^2, σ_{p1}^2, σ_{p2}^2 are, respectively, genetic variance components and phenotypic variance components for trait 1 and trait 2. Standard errors of genetic correlations were estimated following Scheinberg (1966).

1.3 Results

1.3.1 Seed weight effect

Seed weight effect in the first growing season was significant on most seedling absolute growth traits and dry biomass traits but was not significant on ratio traits and some growth increment traits such as NH3-2, NH4-2 and NH4-3 (table 1.1). Stronger effects of seed weight on seedling growth were found in high than in low nutrient level (figure 1.3). However, no significant differences in seed effect were found among the three water treatment levels.

The effect of seed weight decreased with seedling age, as indicated by the decreasing family mean correlation coefficient between seed weight and trait measured over time (table 1.3). Family-mean seed weight did not correlated significantly with 15-year family-mean height or mean diameter growth of the same families growing in the field.

1.3.2 Treatment effects

1.3.2.1 Nutrient effect

Seedlings growing in high nutrient level (200 ppm) had considerably larger size measurements (i.e. 31% larger in height, 39% larger in basal diameter and 119% larger in dry biomass) than seedlings growing in low nutrient level (20 ppm) (table 1.4). Greatly significant differences ($p<0.001$) were detected between the two nutrient levels on 23 growth and biomass traits measured 2-4 months after the treatment was applied (table 1.5). Low nutrient supply not only profoundly retarded seedling size growth, but also delayed the occurrence of secondary needle. The formation of apical terminal bud was promoted by low nutrient supply, especially when it was combined with severe water stress (figure 1.2). The length of seedling growing period averaged 3.71 days shorter under low nutrient level than it did under high nutrient level.

Seedling biomass allocation was noticeably affected by nutrient supply. At the high nutrient level, though root and above ground biomass were considerably larger than those at low nutrient level (table 1.4), shoot/root dry biomass ratio (SB/Rt) was much larger than at low nutrient level (table 1.6). In high nutrient level, seedlings allocated greater proportion of their dry biomass to branches and leaves at the expense of roots compared with that in the low nutrient level. The proportion accounted for by stem in the total dry biomass did not change much across the nutrient treatments. However, the percentage accounted for by stem in the shoot dry biomass was larger at low nutrient level than at high nutrient level. The stem form, as indicated by H/D, only showed minor changes across the two nutrient levels.

1.3.2.2 Water effect

The effect of water treatment on seedling growth was significantly detected for traits of basal diameter and increment, organ dry biomass and some ratio traits but not for traits of seedling height and height increment (table 1.5). Large growth differences were observed between water treatment level W1 (seedlings being watered every two weeks) and level W2 (seedling being watered once a week) or between W1 and W3 (seedling being watered twice a week), but very little differences were found between water level W2 and W3 (table 1.4). Seedling diameter and biomass growth were significantly restrained by soil moisture stress during the growing period. Seedling root/shoot dry biomass ratio (R/S) and height/basal-diameter ratio (H/D) were also significantly affected by water treatment. The greater the soil moisture stress, the higher the ratios of R/S and H/D.

Nutrient-by-water interaction (N x W) was only significant on traits of branch (Br), length of growing period (LGP) and final seedling height measurement (H4) (table 1.5). Low nutrient supply (N1) and severe soil moisture stress (W1) had increasing negative effect on branch development, growth period and the final height growth relative to the other treatment combinations. For other traits, N x W interaction was, however, not significant.

Different seedling traits showed considerable differences in their response to water and nutrient treatments. Seedling height and height increment were largely affected by nutrient treatment, but stable across the three water treatment levels. Stem form (H/D), on the other hand, was only affected by water treatment. Other traits such as seedling diameter, diameter increment and biomass traits were significantly affected by both nutrient and water treatments.

1.3.3 Genetic variation

Genetic variation among the 25 open-pollinated jack pine families was presented by the fixed effect of family classes and the random variation among families within family classes (table 1.5). Family class differentiation was significant for all growth and biomass traits. The average growth of family class

1 (the fast-growing) was always the best, followed by family class 2 (average-growing) and then family class 3 (slow-growing). T-test (table 1.4) indicated that most growth traits were significant between family class 1 and family class 2 or between family class 1 and family class 3. There was no significant difference between family class 2 and family class 3.

The random effect of families within family classes was also significant for most growth traits, but the significance level was less than the effect of family classes on some of the traits. The variance component for families within family classes accounted for 11.35 - 15.18% of the total phenotypic variance in traits of absolute seedling height, 5.61 - 9.29% in traits of seedling basal diameter and 1.99 - 6.63% in traits of seedling dry biomass. For all traits observed, 81.78 - 96.81% of the total phenotypic variance was retained among individuals within families (table 1.7).

The magnitude of genetic variation appeared to vary according to the type of traits observed. Traits of seedling height and height increment exhibited the most genetic variation as shown by their greater significant differences among family classes and greater genetic variance component estimates for families within family class. This was followed by seedling basal diameter that showed considerable differences among family classes and significant genetic variation among families within family classes. Traits of dry biomass measurements were fairly discriminative to family classes differences, but they showed less genetic variation among families within family classes (table 1.7). Ratio trait S/R differed little among family classes and its variance component estimate for families within family classes accounted for only a small portion of total variance.

Environmental conditions under which seedlings were grown presented a certain amount of influence on the magnitude of genetic variation. Both genetic variance component estimates and genetic variation coefficient (for families within family classes) were greater at high nutrient (N2) level than those at low nutrient (N1) level (table 1.8).

Interaction between genetic entries (family classes or families within family classes) and water treatment was negligible for all traits. Interactions between family classes and nutrient treatment were only significant for trait NH3-2 and NH4-2. However, interaction between families within family classes and nutrient treatments were observed for seedling height, basal diameter and, in particular, organ dry biomass (table 1.7).

The performance of family classes was very stable across water and nutrient treatments. For all traits, ranks of the three family classes did not change over different nutrient and water combinations. Despite some significant families/class x nutrient interaction, the performance of families within family classes was also stable. Type B genetic correlations (for families within family classes) for the same trait measured in the two nutrient levels showed little departure from unity for most growth traits (table 1.9). Spearman's family rank correlations for the same trait measured in 6 different nutrient and water treatment combinations were also high and highly great significant (table 1.10). Joint regression analyses indicated that fast-growing families had a tendency, as measured by B_i, to give greater growth response to environment changes due to nutrient and water treatments (environment was indexed by the mean of all families) (table 1.11).

The estimates of heritability were functions of the ANOVA models from which the variance components were derived. Family heritability estimates were highest when ignoring the effects of family classes and seed weights and were lowest when effects of family classes and seed weight were considered (table 1.12). In terms of seedling trait, family heritability estimates were highest for absolute seedling heights (ranging from 0.78 to 0.94), followed by absolute seedling diameters (ranging from 0.60 to 0.85) and then biomass traits (ranging from 0.00 to 0.77). Family heritability estimates were slightly lower for height and diameter increments. The estimate of family heritability was low for R/S ratio (0.13 to 0.16). Narrow-sense heritabilities were high for seedling absolute height and diameter measurements but were low for height and diameter increments and for seedling dry biomass traits.

Genetic correlation estimates among seedling traits were high and positive (table 1.13), indicating the proportional growth among seedling organs with the increase in seedling size.

1.4 Discussion

1.4.1 Seed Weight Effect

The effect of seed weight on conifer seedlings has been reported for a variety of species, including Norway spruce (*Picea abies* (L.) Karst.) (Nanson 1985), Douglas-fir (*Pseudotsuga menziesii var. menziesii* (Mirb.) Franco) (Sorensen and Campbell 1985, 1992; St. Clair et al. 1991), slash pine (*Pinus elliottii* Engelm.) (Surles at el. 1993), maritime pine (*Pinus Pinaster* Ait.) (Lascoux et al. 1992), loblolly pine (Pinus taeda L.) (Robinson and van Buijtenen, 1979, Waxler and van Buijtenen 1981, Dunlap and Barnet 1983), lodgepole pine (*Pinus contorta* spp. *latifolia* Engelm) (Wu 1993), and jack pine (*Pinus banksiana* Lamb.) (Wright et al. 1992). In almost all cases families and individual seedlings from larger seeds often exhibited larger size and higher vigour (Sorensen and Campbell 1985; Surles et al. 1993). Our results with jack pine, with family means, were in agreement with these findings. Our results also indicated that seed weight exerted strong effect on most seedling growth traits and little effect on root/shoot dry biomass and the other ratio traits, which might be the results of cancelation since seed weight effect presented in both the numerator and denominator. In addition, our results indicated that the formation of first-year seedling apical bud was not correlated with seed weight. This could partially suggest that the larger seedling sizes associated with heavy seeds in the first year were primarily due to rapid growth rather than longer growing period.

Smith et al. (1993) observed the influence of environment on the expression of seed weight in slash pine. In their study, the effect of seed weight on seedling height was more significantly expressed in low N treatment than in high N treatment. Our results with jack pine seedling, however, showed the opposite trend. We found higher positive correlation between seed weight and growth trait under high nutrient condition than under low nutrient condition. Perhaps the difference between the studies reflects species variation. However, it could also have suggested that genetic estimates should always be interpreted with caution because they are functions of the reference base population and test environment. In another study of jack pine, Wright et al (1993) found that near one-half of the correlations between traits of seedling root growth and seed weight were significant under well watered treatment condition, and only one-fifth of them were significant under drought treatment.

In many studies so far reported, seed effect on conifer seedling was strongest during the first growing season, then declined to become less significant (Lascoux 1992; St. Clair and Adams 1991; Wu, 1993). In our study, although seed weight effect was significant for most growth traits throughout the experiment, a similar trend was also found by examining the decrease in correlation coefficient estimates between seed weight and growth traits over time in the first growing season (table 1.3). The considerable drop in correlation coefficient for height increment or basal diameter increment would further reflect the smaller effect of seed weight on later growth of jack pine seedling. Similar phenomenon have been reported in lodgepole pine with 110 open-pollinated families (Wu 1993).

Family differences in seed weight may be primarily due to maternal effects and not repeatable. Thus, genetic studies of seedling at young age could present serious bias in estimating genetic variance components, family ranking, heritabilities and genetic gains if the effect of seed weight on seedling performance was strong and not adjusted. In at least a few studies, family differences in seed weight were found to have long lasting effect due to additive genetic differences (Nanson 1985; Surles 1993; Sorensen and Campbell 1992). Thus, the true value of additive genetic variance in seedling traits may lie somewhere between those adjusted and unadjusted for seed weight (St. Clair and Adams 1991). Perhaps the best judgement should be based on an examination of the correlations between seed weight and mature tree performance. In our study, the family correlation between seed weight and 15-year tree height and diameter growth across sites in the field were positive (Pearson correlation coefficient $r=0.31$ and 0.33 respectively, $P>|r|=0.13$ and 0.11, $n=25$), but was not high enough to reject the null hypothesis. However, the fast-growing family class did have the heaviest average seed weight (0.345 g/100 seed), followed by the average-growing family class (0.321 g/100 seeds) and the slow-growing family class (0.307 g/100 seeds). This information might suggest a long but weak effect of seed weight on later tree growth in the field. If this trend holds true, there is the potential benefit in selecting families with heavier seeds in reforestation program.

After adjustment for seed weight, genetic differences of seedling traits among family classes were considerably reduced, so did the genetic variance component estimates for families within family classes. Reduction in estimates of family heritability decreased over time and it either did not change or became slightly greater for a few height and basal diameter traits. These results were in partial agreement with other studies in which estimates of family heritability were lower with seed weight adjustment (St. Clair and Adams 1991; Sorensen and Campbell 1992). The unchanged or even greater heritability estimates after seed weight adjustment for some traits were due to the relative small seed weight effect. After seed weight adjustment, the family-mean correlations between seedling trait and 15-year field tree growth were generally lower than without seed weight adjustment. This might suggest that seed weight adjustment is not necessary in jack pine because it seemed to penalize some genetically superior families with heavier seed weight rather than remove confounding variations (table 1.14).

1.4.2 Treatment effects

Highly significant response of jack pine seedlings to nutrient concentrations in the soil could either suggest the sensitivity of the species to available soil nutrient elements or reflect increased environmental difference caused by nutrient treatment. Nutrient concentration of 200 ppm is in the range of optimum concentration to produce vigorous, well balanced conifer seedlings with intermittent application regimes (Giertych and Farrar 1962; Scarratt 1987). Although the application interval in our experiment was much longer than in other studies, this concentration still appeared to be adequate for first year jack pine seedling since there was no sign of nutrient deficiency during the study. Low nutrient concentration (20 ppm), on the other hand, was apparently below the basic demand of jack pine seedlings for growth since seedlings exhibited visible sign of nitrogen deficiency during the later phase of the study. As our main objective was to observe different genetic expression on juvenile traits among families under different growing conditions, the large environmental difference due to nutrient treatment could be useful for our purpose.

Less significant effect of water treatment on height growth but highly significant effect on basal diameter and dry biomass growth might reflect the water balance dynamics of seedling over time in this study. During the early stage, seedling shoots were tiny. Thus, seedling transpiration was small. However, roots grew rapidly and reached considerable depth into the soil and could utilize water there. With the deep containers used in the study, although the watering interval was as long as two weeks for water treatment level W1 and one week for water treatment level W2, soil was still moist enough to support normal growth.

As seedling grew, soil water consumption increased, but water stress in the soil of treatment level W1 and W2 might not be severe enough to slow down height growth and stem elongation until terminal bud formation occurred in late August. However, with more and more needle appearing at the late stage of the study, water consumption and shortage in the water withheld treatments might be severe enough to retard diameter and dry biomass growth (table 1.15).

Besides their effects on seedling size, the other important effect of nutrient and water treatments was on dry biomass allocation. In this study, significant effects of nutrient and water treatments on R/S were similar to the common trends found in other studies (Cannell et al. 1978; Scarratt 1987; Van Den Driessche 1991; Li et al. 1991). Since biomass allocation is a function of plant size (Ledig and Perry 1965), treatment effects on biomass allocation should be compared on plants of equal size. Following the approach of Li et al.(1991), we checked the effects of nutrient and water on allocation of dry biomass allocation by examining their effect on the parameters of Huxle's (1932) allometric relationships:

$$Y=ax^k \quad \text{or} \quad log(y)= a + k\, log(x) \qquad (1.10)$$

where y is the dry weight of one plant organ (such as stem, needle, or roots), x is the total plant dry weight, and a and k are estimated parameters for intercept and slope, respectively. Our results showed that both a and k were significantly different for nutrient or water treatments. Such results contrast Li et al.(1991) who found that nitrogen effect on dry biomass allocation was significant only in a but not in *k* in loblolly pine. When jack pine seedlings were adjusted to the same size (mean of the total dry biomass of the experiment), greater proportion of total dry biomass was allocated to the above ground organs (leaves, branches and stem) at the expenses of roots under the high nutrient level or at less severe drought conditions (i.e. W3>W2>W1).

The insignificant nutrient-by-water interaction on most traits might have indicated independent effects of the nutrient and water treatment on jack pine seedling growth and/or nutrient and water treatments exert different effect on jack pine seedling at different time. Insignificant nitrogen x water interaction has also been observed in other studies such as in seedlings of Douglas-fir and white-spruce (Van Den Driessche 1991).

1.4.3 Family classes and family effect

Age-age correlation studies indicated that mature tree performance could be predicted with increasing accuracy with the increase of the age of testing plantation (Lambeth 1980). If the 15-year-old field progeny tests in Saskatchewan, which included the families in this study, reliably reflected the real genetic differences among families of jack pine, differences among family classes in this seedling study should, therefore, be the major and most detectable genetic variation since families in this study were from different growing-classes in the field. Comparably, genetic variation among families within family classes (families/family classes) would only reflect a minor and less detectable genetic variation. In this study, the relative greater effect of family classes than the effect of families/classes demonstrated the consistency between the field progeny test and the seedling study in the greenhouse. Thus, there is promise in identifying superior jack pine family group at a very early age (as early as 6 moths).

By considering family classes as fixed genetic effect in the ANOVAs, estimates for additive genetic variance components were reduced considerably (compare table 1.7 and table 1.16). However, the magnitude of additive genetic variance component for families within family classes was still large. Consequently, heritability estimates were high. This could reflect either the inflated differences among families due to maternal effects and/or the uniformity of the testing condition in the greenhouse. Individual heritability estimates were high for absolute height and diameter measurements but were considerable lower for seedling height and diameter increments. This was primarily due to the large proportion of error term in the total phenotypic variance, which might be caused by the growth differences among seedlings within families, comparably larger measuring error and other factors such as the diminishing seed weight effect with seedling age etc..

The insignificant interaction between family classes and treatment (either nutrient or water) illustrated similar response patterns among different jack pine family groups and the high stability of family class performance under different water and nutrient conditions. This result was consistent with reports of other genetic tests in jack pine which also found non-significant G x E interaction (Carter 1990; Adams et al. 1990). Though the high stability of family classes in this study might have been associated with the big genetic differences among family classes as mentioned above, the practical implication to early selection would be that genetically superior and inferior groups of jack pine families could be identified, as long as their genetic differences were large, regardless of the nutrient and water conditions under which seedlings were tested.

Interaction between family within family classes and treatments might not be as important as the interaction between family classes and treatment because practically only the superior group of families will be retained in seedling seed orchard in most tree improvement program (King 1973; Klein 1982; Carter et al. 1990). However, when specific family ranking is important, it would be necessary to consider families/classes x treatment interaction. In this study, families/classes x water treatment interaction was not significant, but families/classes x nutrient treatment interactions were significant for almost all traits observed. The significant families/classes x nutrient interaction resulted in some change in family ranking both between and within family classes (table 1.17). Thus, it would necessitate the selection of early testing nutrient condition for a more precise early test. Significant family x nitrogen interaction has been reported in slash pine (Smith et al. 1992) and loblolly pine (Li et al. 1991). Significant family x water interaction was also found in loblolly pine (Cannell et al. 1978). The present study is the first report on family x water and family x nutrient interactions in seedlings of jack pine.

The slightly greater genetic variation among families in the high nutrient level might also give some hint on the selection of early testing environment in jack pine. Favourable nutrient and water condition seemed to have promoted the ontogenic development of jack pine seedlings as shown by the bigger seedling size as well as the earlier and more frequent occurrence of secondary needles.

Stronger genetic control on height than on other seedling traits might indicate the superiority of height for early selection since seedling height growth has also been demonstrated to give the highest early-mature correlations (Greenwood and Volkaert 1992). Although seedling penology is under strong genetic control and gives high age-age correlation in other species (Cannell et al. 1981), bud formation and the duration of growth period in this study differed very little among the three family classes. Therefore, their predictability of mature growth would be limited. This is also true for S/R ratio.

High genetic correlations among seedling traits resulted in similar genetic variation patterns of different seedling traits, although there were some differences in scales. High and positive genetic correlation among seedling traits may, to some degree, limit the use multi-seedling-trait indirect selection (White and Hodge 1991) in jack pine. This is because there would be relatively less additional information by adding more seedling traits in a multi-trait indirect selection equation.

In summary, the results of this study indicated that both nutrient and water treatments had significant effects on growth of jack pine seedlings, but their interaction was negligible. Genetic control of first-year jack pine seedling was strong which might have been inflated by maternal effect. Insignificant family class x treatment (either nutrient or water) interaction coupled with significant families/classes x nutrient treatment interaction suggested that the role of environment in early testing is not important in identifying genotypic (family) groups when genetic differences are large. However, when genetic differences are small, nutrient conditions are important in identifying superior families.

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Table 1.1 Abbreviation and description of seedling traits

H0	height from soil surface to the first leaf at two months.
H1	height from soil surface to the top of leaves at two months (before treatment began).
H2	height from soil surface to apical meristem at four month (two months after treatment).
D1	basal diameter at four months.
H3	height from soil surface to apical meristem at five months.
D2	diameter at five months.
H4	height from soil surface to apical meristem at six months (before final harvest).
D3	diameter at six months.
Ne	leaf dry biomass at harvest.
Br	branch dry biomass at harvest.
Ust	upper stem (stem with leaves and branches) dry biomass at harvest.
Lst	lower stem (stem without leaves and branches) dry biomass at harvest.
Rt	root dry biomass at harvest.
SB	shoot dry biomass at harvest (SB = Ne + Br + Ust + Lst).
Tbio	Total dry biomass at harvest (Tbio = SB + Rt).

NH1-0 = H1 - H0.
NH2-0 = H2 - H0.
NH3-0 = H3 - H0.
NH4-0 = H4 - H0.
NH3-2 = H3 - H2.
NH4-2 = H4 - H2.
NH4-3 = H4 - H3.
ND2-1 = D2 - D1.
ND3-1 = D3 - D1.
ND3-2 = D3 - D2.
S/R = SB / Rt.
H/D = H4 / D3.

Table 1.2 Abbreviation and description of treatment

N1	nutrient treatment level 1 (N-P-K 20 ppm).
N2	nutrient treatment level 2 (N-P-K 200 ppm).
W1	water treatment level 1 (watering interval = 2 weeks).
W2	water treatment level 2 (watering interval = 1 week).
W3	water treatment level 3 (watering interval =3.5 days).
N1W1	combination of nutrient level 1 and water level 1.
N1W2	combination of nutrient level 1 and water level 2.
N1W3	combination of nutrient level 1 and water level 3.
N2W1	combination of nutrient level 2 and water level 1.
N2W2	combination of nutrient level 2 and water level 2.
N2W3	combination of nutrient level 2 and water level 3.

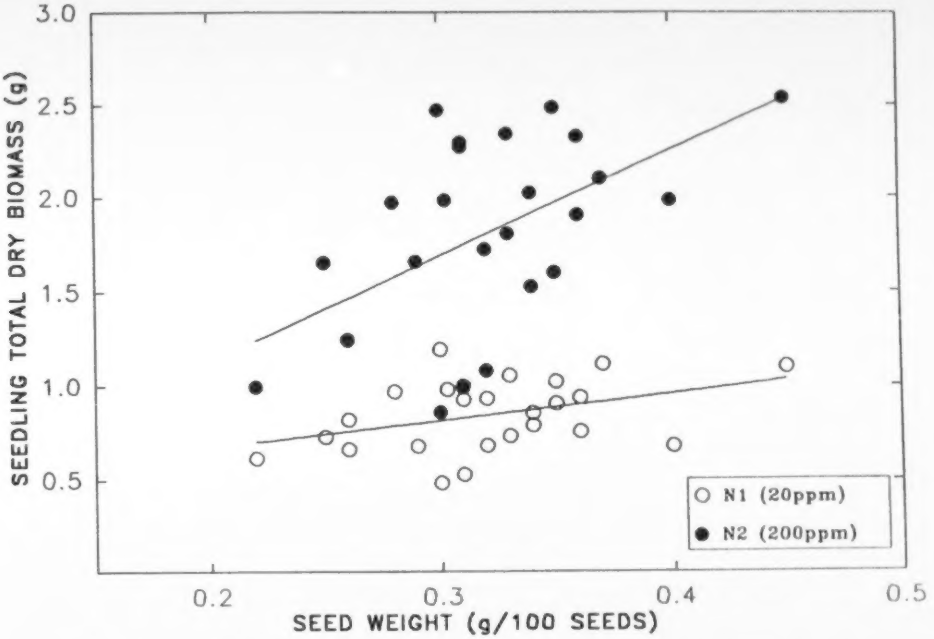

Figure 1 Relationship between family mean seedling total dry biomass and family mean seed weight under to nutrient levels (N1, N2).

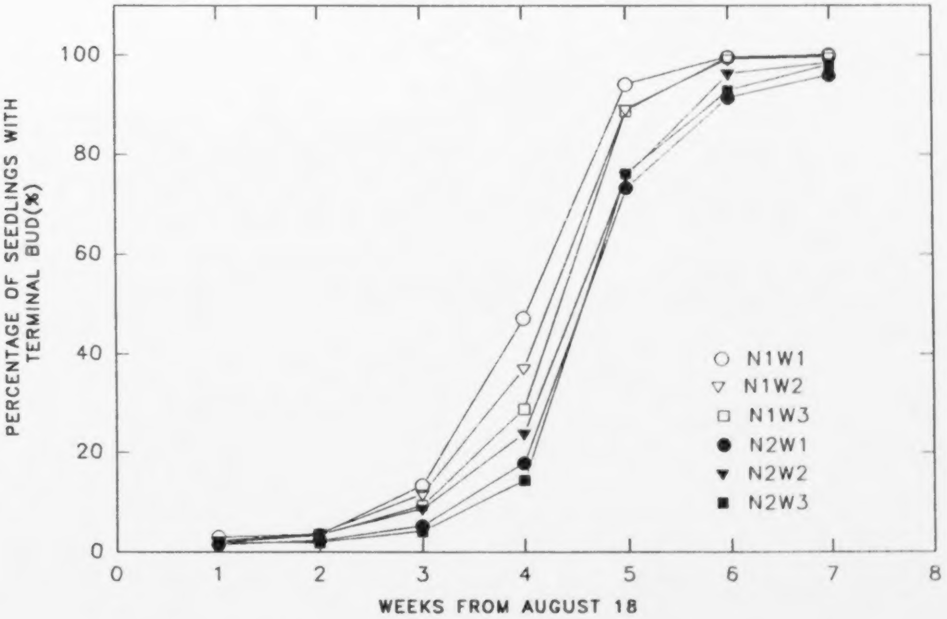

Figure 2 Terminal bud formation of jack pine seedlings was promoted by low nutrient supply and soil water stress.

Table 1.3 **Pearson correlation coefficients and the corresponding significant levels between family mean seed weight (g/100 seeds) and family mean value of seedling measurements (n=25) in the low (N1) and high (N2) nutrient treatment levels and as they were pooled [a]**

	H0	H1	H2	H3	H4	NH1-0	NH2-0	NH3-0
N1	0.66**	0.57**	0.48*	0.45*	0.44*	0.46*	0.34	0.33
	0.00	0.00	0.02	0.02	0.03	0.02	0.10	0.11
N2	0.68**	0.65**	0.55**	0.54**	0.54**	0.57**	0.44*	0.46*
	0.00	0.00	0.00	0.01	0.01	0.00	0.03	0.02
N1&N2	0.70**	0.63**	0.54**	0.53**	0.51**	0.54**	0.42*	0.43*
	0.00	0.00	0.01	0.01	0.01	0.01	0.04	0.03

	NH4-0	NH3-2	NH4-2	NH4-3	D1	D2	D3	ND2-1
N1*	0.32	0.23	0.21	-0.15	0.64**	0.59**	0.53**	0.17
	0.12	0.27	0.31	0.48	0.00	0.00	0.01	0.42
N2	0.45*	0.40*	0.39	-0.07	0.70**	0.65**	0.58**	0.42*
	0.02	0.05	0.06	0.73	0.00	0.00	0.00	0.04
N1&N2	0.42*	0.35	0.34	-0.11	0.72**	0.67**	0.61**	0.40
	0.04	0.08	0.10	0.59	0.00	0.00	0.00	0.05

Note: *N stands for nutrient treatment. N1— low N level (20 ppm), N2— hight N level (200 ppm), N1 & N2 —N1 and N2 combined.

[a] see table 1.1 for description of traits.

Table 1.3 (continued). Pearson correlation coefficients and the corresponding significant levels between family mean seed weight (g/100 seeds) and family mean value of seedling measurements (n=25) in the low (N1) and high (N2) nutrient treatment levels and as they were pooled [a]

	ND3-1	ND3-2	Ne	Ust	Lst	St	Br	Rt
N1	0.22	0.22	0.36	0.34	0.52**	0.42*	0.49*	0.50*
	0.28	0.28	0.08	0.10	0.01	0.04	0.01	0.01
N2	0.34	0.32	0.52**	0.55**	0.60**	0.58**	0.50*	0.57**
	0.08	0.12	0.01	0.00	0.00	0.00	0.01	0.00
N1&N2	0.37	0.36	0.49*	0.52**	0.61**	0.56**	0.51**	0.58**
	0.07	0.08	0.01	0.01	0.00	0.00	0.01	0.00

	SB	Tbio	LGP	S/R	H/D
N1*	0.40*	0.45*	0.04	-0.03	0.14
	0.05	0.02	0.86	0.89	0.51
N2	0.56**	0.57	0.05	-0.10	0.13
	0.00	0.00	0.79	0.63	0.52
N1&N2	0.53**	0.55**	0.05	-0.08	0.16
	0.01	0.00	0.81	0.72	0.46

Note: *N stands for nutrient treatment. N1— low N level (20 ppm), N2— hight N level (200 ppm).

N1 & N2 —N1 and N2 combined.

[a] see table 1.1 for description of traits.

Table 1.4 **Means of seedling trait measured under different levels of nutrient(N) treatment, water (W) treatments and family class (C)[a]**

		H0	H1	H2	H3	H4	NH2-0	NH3-0	NH4-0	NH3-2
N	1	16.38a	54.50a	36.16b	40.33b	42.35b	19.79b	23.96b	25.97b	4.15b
	2	16.38a	55.07a	44.07a	51.71a	54.21a	27.65a	35.29a	37.76a	7.59a
W	1	16.46a	55.28a	40.34a	46.10a	48.12a	23.83a	29.58a	31.60a	5.75a
	2	16.20a	55.18a	40.37a	46.21a	48.77a	24.16a	29.99a	32.53a	5.83a
	3	16.47a	53.89b	39.64a	45.75a	47.95a	23.16a	29.29a	31.47a	6.04a
C	1	17.12a	58.52a	44.36a	52.11a	54.35a	27.24a	35.00a	37.24a	7.74a
	2	16.35b	54.37b	39.38b	44.85b	46.99b	23.09b	28.57b	30.71b	5.43b
	3	15.74b	51.39b	36.60b	41.03b	43.31b	20.87b	25.30b	27.54b	4.43b

continued

		NH4-2	NH4-3	D1	D2	D3	ND2-1	ND3-1	ND3-2	Ne
N	1	6.13b	1.98b	0.96b	1.09b	1.26b	0.14b	0.30b	0.17b	0.38b
	2	9.96a	2.37a	1.21a	1.44a	1.72a	0.23a	0.51a	0.28a	0.94a
W	1	7.64a	1.83b	1.06a	1.21b	1.36b	0.15b	0.30b	0.15b	0.57b
	2	8.30a	2.48a	1.09a	1.30a	1.55a	0.21a	0.46a	0.25a	0.70a
	3	8.20a	2.21ab	1.09a	1.29a	1.56a	0.20a	0.47a	0.27a	0.72a
C	1	9.99a	2.26a	1.15a	1.36a	1.62a	0.21a	0.47a	0.26a	0.80a
	2	7.57b	2.16b	1.07b	1.24b	1.46b	0.18b	0.40b	0.22b	0.64b
	3	6.55b	2.09b	1.03b	1.19b	1.39b	0.16b	0.36b	0.19b	0.55b

continued

		Br	Ust	Lst	Rt	SB	Tbio	LGP	S/R	H/D
N	1	0.03b	0.03b	0.02b	0.39b	0.47b	0.87b	96.60b	1.34b	34.23a
	2	0.20a	0.09a	0.04a	0.52a	1.29a	1.81a	100.31a	2.93a	32.44b
W	1	0.09b	0.05b	0.03b	0.40b	0.74b	1.14b	98.16b	1.93b	35.65b
	2	0.12a	0.07a	0.03a	0.49a	0.93a	1.42a	98.07b	2.17a	32.46a
	3	0.14a	0.07a	0.03a	0.49a	0.97a	1.46a	99.14a	2.32a	31.90a
C	1	0.16a	0.08a	0.04a	0.55a	1.07a	1.62a	98.88a	2.22a	34.71a
	2	0.10b	0.06b	0.03b	0.45b	0.83b	1.28b	98.67a	2.08a	33.06ab
	3	0.10b	0.05b	0.03b	0.38b	0.73b	1.11b	97.83a	2.12a	32.17b

Note: no significant difference (p=0.05) exists among means with same letter and significant difference (p=0.05) exists among means with different letter. [a] see table 1.1 for description of traits.

Table 1.5 F values and the corresponding significant levels for testing the effect of nutrient treatment(N), water treatment(w), family class(C) and their interactions[a]

TRAIT	N	W	N*W	C	C*N	C*W	C*N*W
H0	0.00	0.97	0.01	2.04	0.21	0.85	0.33
	0.99	0.40	0.99	0.11	0.82	0.50	0.86
H2	5.49**	1.95	5.10	7.43**	0.65	1.11	0.51
	0.00	0.20	0.09	0.00	0.53	0.37	0.73
H3	106.70**	0.54	5.83	11.44**	2.04	1.10	0.32
	0.00	0.60	0.05	0.00	0.15	0.37	0.86
H4	103.19**	1.33	7.65*	11.40**	1.73	0.92	0.30
	0.00	0.32	0.03	0.00	0.20	0.46	0.88
NH2-0	70.22**	2.10	1.38	6.96**	0.86	0.98	0.55
	0.00	0.17	0.29	0.00	0.44	0.43	0.70
NH3-0	102.92**	0.84	2.85	11.37**	2.61	1.02	0.31
	0.00	0.47	0.11	0.00	0.10	0.41	0.87
NH4-0	96.91**	2.09	3.92	11.18**	2.30	0.87	0.31
	0.00	0.19	0.06	0.00	0.12	0.49	0.87
NH3-2	113.24**	0.65	2.57	13.13**	6.12**	0.96	1.02
	0.00	0.55	0.12	0.00	0.01	0.44	0.41
NH4-2	79.23**	1.52	3.01	14.80**	6.69**	0.49	0.24
	0.00	0.25	0.08	0.00	0.01	0.75	0.91
D1	156.33**	1.68	0.25	4.71*	0.12	1.13	0.35
	0.00	0.22	0.78	0.02	0.89	0.36	0.85
D2	114.47**	6.52**	0.04	6.15**	0.86	1.03	0.63
	0.00	0.01	0.96	0.01	0.44	0.40	0.64
D3	124.19**	15.55**	1.23	7.19**	0.61	2.26	0.22
	0.00	0.00	0.31	0.00	0.55	0.08	0.93
ND2-1	23.07**	6.28**	0.36	5.59*	2.33	0.38	0.87
	0.00	0.01	0.71	0.01	0.12	0.82	0.49
ND3-1	45.68**	18.38**	2.14	6.51**	0.90	2.09	0.49
	0.00	0.00	0.14	0.01	0.42	0.09	0.74
Ne	97.49**	11.54**	1.06	6.92**	1.67	1.85	0.52
	0.00	0.00	0.37	0.00	0.21	0.14	0.72
Ust	65.89**	9.70**	0.91	6.95**	3.00	0.80	0.38
	0.00	0.00	0.42	0.00	0.07	0.53	0.82
Lst	61.90**	12.93**	1.57	7.16**	1.01	0.66	0.16
	0.00	0.00	0.24	0.00	0.38	0.62	0.96
St	66.96**	11.18**	0.98	7.52**	2.45	0.79	0.32
	0.00	0.00	0.40	0.00	0.11	0.54	0.87
Br	56.74**	6.31**	5.35*	3.42	3.14	2.15	2.04
	0.00	0.01	0.02	0.05	0.06	0.09	0.11
Rt	16.89**	6.03*	0.36	7.88**	0.75	1.94	0.87
	0.00	0.01	0.70	0.00	0.48	0.12	0.49

continued

Table 1.5 continued

TRAIT	N	W	N*W	C	C*N	C*W	C*N*W
SB	92.84** 0.00	11.05** 0.00	0.96 0.41	6.88** 0.00	2.34 0.12	1.80 0.15	0.35 0.84
Tbio	71.65** 0.00	9.36** 0.00	0.67 0.53	7.25** 0.00	1.83 0.18	1.81 0.14	0.41 0.80
S/R	166.04** 0.00	15.65** 0.00	0.19 0.83	1.51 0.24	0.38 0.69	1.44 0.24	0.62 0.65
H/D	4.10 0.06	15.57** 0.00	1.61 0.23	3.91* 0.04	0.79 0.47	2.75* 0.04	0.60 0.66
LGP	44.18** 0.00	3.73 0.06	6.96* 0.01	0.31 0.74	0.98 0.39	0.20 0.94	3.04* 0.03

[a] see table 1.1 for description of traits.

Table 1.6 Jack pine seedling relative dry biomass allocation and S/R ratios under different nutrient (N) and water (W) treatment conditions [a]

Trait	N1 (%)	N2 (%)	W1 (%)	W2 (%)	W3 (%)
Ne	44.46	52.24	49.56	49.36	49.91
Br	3.49	12.51	8.05	8.89	9.38
Rt	45.40	29.34	35.42	34.70	33.73
St	6.65	7.16	6.97	7.04	6.97
SB	54.60	70.65	64.53	65.30	66.27
R/S	0.83	0.42	0.55	0.53	0.51
H/D	12.18	10.13	10.80	10.78	10.52

NOTE: N1 – low nutrient level; N2 – high nutrient level; W1 – water every two weeks; W2– water once a week; and W3 – water twice a week.

[a] see table 1.1 for description of traits.

Table 1.7 Variance component estimates for family within family class (percent accounted for the total phenotypic variance is in the bracket)[a]

TRAIT	F/C	N*F/C	W*F/C	N*W*F/C	ERROR
H0	1.5414 (15.18)**	0.0152 (0.15)	0	0	8.5952 (84.67)
H1	9.7023 (14.66)**	1.3410 (2.03)	0.2245 (0.34)	0	54.9294 (82.98)
H2	14.1802 (14.38)**	2.6842 (2.74)*	0	1.0901 (1.11)	80.2455 (81.78)
H3	18.1705 (11.47)**	3.5236 (2.22)	0	0.5769 (3.66)	136.0869 (85.93)
H4	18.6511 (11.35)**	2.3102(1.41)	0	2.8062 (1.71)	140.5817 (85.54)
NH2-0	9.9493 (12.35)**	2.4327 (3.02)*	0	0.6682 (0.83)	67.5020 (83.80)
NH3-0	13.9585 (10.03)**	2.8773 (2.07)	0	0	122.3643 (87.91)
NH4-0	14.7041 (10.05)**	1.9145 (1.31)	0	1.9153 (1.31)	127.7037 (87.33)
NH3-2	1.3652 (5.87)*	0.2366(1.02)	0.0715 (0.31)	0	21.5602 (92.80)
NH4-2	1.3953 (5.38)*	0	0	0.0193(0.07)	24.4954 (94.55)
D1	4.83 X 10^{-3} (9.29)**	9.71X 10^{-4}(1.87)	0	1.67 X 10^{-3} (3.21)	0.0445 (85.62)
D2	7.03 X 10^{-3} (7.27)*	2.60 X 10^{-3} (2.69)	0	2.55 X 10^{-3} (2.64)	0.0845 (87.40)
D3	0.01011 (5.61)*	4.88 X 10^{-3} (2.71)	0	0.01003 (5.57)**	0.1551 (86.11)
ND2-1	3.13 X10^{-4} (1.34)	7.20 X 10^{-4} (3.08)*	0	0	0.0224 (95.59)
ND3-1	1.45 X10^{-3} (1.93)	2.79 X10^{-3} (3.71)*	0	2.94 X10^{-3}	0.0680 (90.45)
ND3-2	2.85 X10^{-4} (0.71)	8.56 X10^{-4} (2.14)	0	1.812 X 10^{-3} (4.52)	0.03712 (92.63)
Ne	0.01086 (6.33)*	0.009575 (5.58)**	0	1.7483 X10^{-3} (1.02)	0.1494 (87.06)
Ust	1.02 X10^{-4} (4.16)	8.26 X 10^{-5} (3.35)*	0	7.32 X 10^{-5} (2.97)	0.00221 (89.52)
Lst	1.99 X10^{-4} (5.16)*	2.01 X 10^{-5} (5.18)**	0	6.16 X 10^{-6} (1.55)	0.00337 (87.33)
St	2.00 X 10^{-4} (4.43)	1.66 X 10^{-4} (3.69)*	0	1.34 X 10^{-4} (2.98)	0.00400 (88.91)
Rt	4.87 X 10^{-3} (4.56)*	1.88 X 10^{-3} (1.76)	0	8.97 X10^{-4} (0.84)	0.09901 (92.84)
Br	6.61 X10^{-4}(1.99)	2.62 X10^{-3} (7.88)**	4.28 X10^{-4} (1.29)	1.54 X 10^{-4}(0.46)	0.0294 (88.39)
SB	0.01783 (4.88)*	0.02287 (6.25)**	1.19 X10^{-3} (0.33)	2.74 X10^{-3} (0.75)	0.3208 (87.79)
Tbio	0.0417 (5.08)*	0.0353 (4.30)*	0	6.27 X10^{-3} (0.76)	0.7381 (89.86)
S/R	4.91 X10^{-3} (0.56)	0.0167 (1.91)	0	5.31 X10^{-3} (0.61)	0.8465 (96.81)
H/D	1.9580 (5.29)*	1.8653 (5.04)*	0.2061(0.56)	0	33.0020(89.12)
LGP	6.787 (12.23)**	1.6229 (2.92)*	0	0	47.1028 (84.85)

[a] See table 1.1 for description of traits.

Note: * indicates significant at probability level of 0.05 and ** indicates significant at probability level of 0.01. F/C, N*F/C, N*W*F/C and ERROR are respectively effect of families within family class, nutrient x families within family class, water x families within family class, nutrient x water x families within family class and error term.

Table 1.8 **Estimates of variance components and genetic variation coefficients (g.v.c.) for family within family class in high (N2) and low (N1) nutrient levels**[a]

TRAIT		H2	H3	H4	NH2-0	NH3-0	NH4-0	NH3-2
N1	σ^2	11.6045	14.8080	15.3489	7.3951	10.7752	11.2678	1.0110
	g.v.c.	9.51	9.62	9.34	13.89	13.85	13.08	24.53
N2	σ^2	22.1444	28.7073	26.6703	17.5200	22.9465	22.1337	2.2065
	g.v.c.	10.61	10.30	9.43	14.99	13.44	12.28	19.49

continued

TRAIT		D1	D2	D3	ND2-1	ND3-1	ND3-2	Ne
N1	σ^2	0.00321	0.00428	0.00532	0.00050	0.00060	0.00003	0.00305
	g.v.c.	5.97	6.00	5.82	16.37	8.10	3.45	15.26
N2	σ^2	0.00846	0.01512	0.02480	0.00158	0.00802	0.00234	0.03771
	g.v.c.	7.59	8.53	9.11	17.22	17.33	17.10	20.20

continued

TRAIT		Ust	Lst	St	Br	Rt	SB	Tbio
N1		0.00003	0.00001	0.00006	0.00007	0.00228	0.00467	0.01252
	g.v.c.	14.73	14.77	14.07	28.04	12.38	14.82	13.16
N2	σ^2	0.00034	0.00007	0.00067	0.00659	0.01129	0.07706	0.14240
	g.v.c.	20.29	20.49	19.54	40.00	19.77	21.21	20.33

Note: σ^2 srands for variance components estimats for family within family class and g.v.c. is the genetic variation coefficient obtained with the foemula:

$$g.v.c.=\frac{\sigma}{\bar{X}}x100\%$$

[a] See table 1.1 for description of traits and table 1.2 for description of treatments.

Table 1.9 Estimates of type B genetic correlations (r_g) for the same seedling traits measured in the two nutrient treatment levels[a]

Trait	r_g	Trait	r_g
H0	0.99	ND2-1	0.36
H1	0.90	ND3-1	0.68
H2	0.88	ND3-2	1.00
H3	0.88	Ne	0.98
H4	0.92	Ust	1.00
NH2-0	0.88	Lst	0.79
NH3-0	0.89	St	0.97
NH4-0	0.94	Br	1.00
NH3-2	1.00	Rt	0.97
NH4-2	1.00	SB	0.95
D1	0.93	Tbio	1.00
D2	0.88	LGP	0.88
D3	0.89	H/D	0.52

[a] See table 1.1 for description of traits.

Note: type B genetic correlations were estimated using the method of Yamada (1962):

$$r_g = \frac{\sigma^2_{m(l)}}{\sigma^2_{m(l)} + \sigma^2_{m(l)\bullet j} - \frac{(\sigma_{m(l)1} - \sigma_{m(l)2})^2}{2}}$$

where $\sigma^2_{m(l)}$ is the variance component estimated for family within family class using combined data.

$\sigma^2_{m(l)\bullet j}$ is the variance component estimated for family/class x nutrient interaction,

$\sigma^2_{m(l)1}$ is the variance component estimated for family within family class in nutrient level 1 (N1), and

$\sigma^2_{m(l)2}$ is the variance component estimated for family within family class in nutrient level 2 (N2).

Table 1.10 Spearman family rank correlations among 6 combinations of nutrient and water treatment levels in seedling height (H4) (upper diagonal) and seedling total dry biomass growth (Tbio)(lower diagonal) with the significant probability levels in brackets[a].

	N1W1	N1W2	N1W3	N2W1	N1W2	N2W3
N1W1		0.86 (0.00)	0.90 (0.00)	0.79 (0.00)	0.82 (0.00)	0.83 (0.00)
N1W2	0.65 (0.00)		0.90 (0.00)	0.72 (0.00)	0.75 (0.00)	0.77 (0.00)
N1W3	0.75 (0.00)	0.73 (0.00)		0.72 (0.00)	0.81 (0.00)	0.78 (0.00)
N2W1	0.51 (0.01)	0.58 (0.00)	0.62 (0.00)		0.58 (0.00)	0.77 (0.00)
N2W2	0.73 (0.00)	0.65 (0.00)	0.68 (0.00)	0.62 (0.00)		0.75 (0.00)
N2W3	0.69 (0.00)	0.66 (0.00)	0.77 (0.00)	0.66 (0.00)	0.68 (0.00)	

[a] See table 1.1 for description of traits and table 1.2 for description of treatments.

Table 1.11 Family stability (Bi) estimates with different traits (using mean of all families as site index)

FAMILY CIASS	FAMILY CODE	H3	H4	D3	TBIO
1 (fast-growing)	233	1.452	1.406	1.165	1.096
	354	1.533	1.443	1.306	1.373
	362	0.914	0.924	1.525	1.436
	546	0.943	0.926	1.193	1.316
	353	1.434	1.301	0.798	0.919
	343	1.302	1.264	1.121	1.268
	216	0.975	0.979	0.934	0.918
	446	0.457	0.488	0.885	1.061
	mean	1.126	1.091	1.116	1.173
2 (average-growing)	655	1.050	0.989	0.632	0.732
	166	1.221	1.160	1.133	1.193
	544	0.886	0.942	1.386	1.014
	255	0.743	0.677	0.327	0.399
	215	1.257	1.194	1.098	0.926
	414	1.504	1.425	1.218	1.507
	456	1.207	1.197	1.173	1.528
	256	0.836	0.796	0.980	0.485
	632	0.424	0.528	0.420	0.409
	mean	1.014	0.990	0.930	0.910
3 (slow-growing)	452	0.738	0.707	0.767	0.732
	313	1.012	1.010	0.769	0.820
	324	1.104	1.1070	1.281	1.245
	152	0.469	0.403	0.493	0.340
	533	0.701	0.861	1.131	0.529
	421	0.960	0.998	1.327	1.313
	514	0.391	0.521	0.461	0.409
	212	1.114	1.057	1.126	1.032
	mean	0.811	0.740	0.919	0.803

Note: H3, H4, D3 and TBIO are respectively seedling height at 5 months, height at 6 months, basal diameter at 6 months and total dry biomass.

Table 1.12 **Family (h_f^2) and individual (h_i^2) heritability estimates for seedling traits under different situations[a].**

Trait	Fami. class not considered seed weight not adjusted		Fami. class considered seed weight not adjusted		Fami. class considered seed weight adjusted	
	h_f^2	h_i^2	h_f^2	h_i^2	h_f^2	h_i^2
H0	0.90±0.05	0.67±0.07	0.88±0.05	0.58±0.08	0.79±0.10	0.34±0.08
H1	0.94±0.02	1.21±0.06	0.86±0.06	0.59±0.09	0.79±0.09	0.39±0.09
H2	0.90±0.04	0.86±0.05	0.83±0.07	0.58±0.09	0.81±0.09	0.47±0.09
H3	0.89±0.05	0.83±0.05	0.81±0.08	0.46±0.09	0.78±0.10	0.38±0.09
H4	0.90±0.04	0.82±0.06	0.82±0.08	0.45±0.09	0.80±0.09	0.39±0.09
NH2-0	0.88±0.04	0.74±0.07	0.80±0.08	0.49±0.09	0.80±0.09	0.47±0.09
NH3-0	0.88±0.05	0.73±0.07	0.80±0.09	0.40±0.09	0.80±0.09	0.39±0.09
NH4-0	0.89±0.05	0.72±0.07	0.81±0.08	0.40±0.09	0.82±0.09	0.40±0.09
NH3-2	0.84±0.07	0.49±0.09	0.73±0.10	0.24±0.07	0.75±0.11	0.23±0.07
NH4-2	0.86±0.06	0.45±0.08	0.76±0.11	0.22±0.06	0.76±0.11	0.22±0.06
NH4-3	0.96±0.27	0.09±0.03	0.50±0.26	0.08±0.03	0.50±0.26	0.08±0.03
D1	0.85±0.09	0.51±0.09	0.76±0.10	0.38±0.09	0.63±0.10	0.17±0.07
D2	0.80±0.10	0.45±0.09	0.69±0.13	0.29±0.09	0.55±0.13	0.15±0.07
D3	0.76±0.12	0.38±0.09	0.67±0.18	0.21±0.08	0.67±0.18	0.23±0.09
ND2-1	0.45±0.34	0.11±0.07	0.30±0.30	0.05±0.06	0.29±0.42	0.05±0.06
ND3-1	0.53±0.23	0.16±0.08	0.32±0.31	0.08±0.07	0.32±0.31	0.08±0.07
ND3-2	0.45±0.41	0.08±0.06	0.17±0.41	0.03±0.06	0.17±0.41	0.03±0.06
Ne	0.69±0.13	0.41±0.11	0.58±0.18	0.23±0.10	0.53±0.20	0.21±0.10
Br	0.27±0.30	0.10±0.11	—	—	0.22±0.33	0.06±0.09
Ust	0.62±0.14	0.28±0.10	0.52±0.21	0.16±0.08	0.48±0.21	0.13±0.08
Lst	0.69±0.12	0.38±0.10	0.54±0.20	0.19±0.09	0.51±0.20	0.15±0.08
St	0.66±0.13	0.32±0.10	0.53±0.20	0.17±0.09	0.58±0.20	0.16±0.08
Rt	0.77±0.14	0.32±0.08	0.63±0.16	0.17±0.07	0.58±0.16	0.13±0.06
SB	0.61±0.15	0.33±0.11	0.50±0.21	0.18±0.10	0.53±0.21	0.18±0.09
Tbio	0.68±0.15	0.34±0.10	0.57±0.19	0.19±0.09	0.59±0.19	0.18±0.08

[a] See table 1.1 for description of traits.

Table 1.13 Estimates of genetic correlation (upper diagonal) and standard error (lower diagonal) among jack pine seedling traits[a]

	H0	H1	H4	NH1-0	NH4-0	NH4-2	D1	D3	ND3-1	Ne	Ust	St	Rt	SB	Tbio	H/D	LGP
H0		0.86	0.66	0.73	0.51	0.40	0.83	0.79	0.66	0.59	0.64	0.73	0.80	0.65	0.69	0.33	-0.04
H1	0.06		0.89	0.98	0.80	0.65	0.89	0.97	0.93	0.81	0.90	0.94	0.95	0.87	0.89	0.54	0.11
H4	0.28	0.04		0.90	0.98	0.85	0.82	0.93	0.92	0.92	0.97	0.97	0.94	0.95	0.95	0.80	0.04
NH1-0	0.19	0.00	0.03		0.85	0.69	0.84	0.96	0.96	0.83	0.93	0.95	0.93	0.88	0.90	0.58	0.17
NH4-0	0.47	0.12	0.00	0.07		0.87	0.74	0.87	0.90	0.92	0.96	0.94	0.88	0.93	0.92	0.84	0.05
NH4-2	0.62	0.30	0.07	0.26	0.05		0.62	0.69	0.68	0.82	0.78	0.76	0.78	0.80	0.80	0.77	-0.23
D1	0.13	0.05	0.09	0.09	0.17	0.36		0.95	0.74	0.75	0.84	0.89	0.89	0.83	0.84	0.36	0.08
D3	0.19	0.02	0.03	0.03	0.06	0.27	0.02		0.92	0.87	0.96	0.99	0.98	0.93	0.95	0.53	0.15
ND3-1	0.45	0.10	0.07	0.08	0.08	0.35	0.29	0.04		0.92	0.98	0.99	0.97	0.95	0.96	0.67	0.23
Ne	0.42	0.13	0.03	0.11	0.03	0.11	0.18	0.06	0.05		0.91	0.91	0.95	0.98	0.97	0.67	0.30
St1	0.39	0.07	0.01	0.05	0.01	0.17	0.09	0.01	0.02	0.03		0.99	0.94	0.94	0.94	0.64	0.11
St	0.27	0.04	0.01	0.03	0.02	0.18	0.05	0.00	0.02	0.03	0.00		0.97	0.95	0.96	0.60	0.10
Rt	0.19	0.04	0.03	0.05	0.07	0.17	0.07	0.01	0.03	0.02	0.02	0.01		0.99	1.00	0.56	0.00
SB	0.36	0.09	0.02	0.08	0.02	0.13	0.10	0.02	0.03	0.00	0.01	0.01	0.00		1.00	0.63	0.10
Tbio	0.30	0.07	0.02	0.06	0.03	0.14	0.09	0.01	0.03	0.00	0.02	0.01	0.00	0.00		0.61	0.07
H/D	0.72	0.46	0.17	0.42	0.14	0.25	0.80	0.70	0.73	0.44	0.52	0.56	0.64	0.51	0.55		-0.17
LGP	0.82	0.78	0.83	0.77	0.84	0.79	0.89	0.91	1.00	0.91	0.96	0.94	0.96	0.93	0.93	0.88	

[a]See table 1.1 for description of seedling traits

Table 1.13a **Estimates of phenotypic correlation (upper diagonal) and standard error (lower diagonal) among jack pine seedling traits**[a]

	H0	H1	H4	NH1-0	NH4-0	NH4-2	D1	D3	ND3-1	Ne	Ust	St	Rt	SB	Tbio
H0		0.64	0.33	0.31	0.12	0.07	0.25	0.18	0.08	0.15	0.14	0.19	0.16	0.16	0.16
H1	0.01		0.60	0.93	0.49	0.26	0.52	0.42	0.22	0.36	0.39	0.41	0.38	0.37	0.39
H4	0.02	0.01		0.59	0.98	0.77	0.78	0.78	0.58	0.79	0.81	0.81	0.64	0.79	0.77
NH1-0	0.01	0.00	0.01		0.55	0.29	0.52	0.43	0.24	0.38	0.41	0.42	0.40	0.38	0.40
NH4-0	0.01	0.01	0.00	0.01		0.79	0.76	0.78	0.59	0.80	0.82	0.81	0.63	0.79	0.77
NH4-2	0.01	0.02	0.02	0.06	0.10		0.57	0.64	0.53	0.70	0.69	0.69	0.61	0.69	0.69
D1	0.01	0.01	0.03	0.02	0.08	0.01		0.84	0.48	0.74	0.77	0.79	0.63	0.77	0.75
D3	0.00	0.01	0.01	0.02	0.08	0.05	0.01		0.88	0.84	0.87	0.89	0.75	0.86	0.86
ND3-1	0.00	0.01	0.02	0.01	0.03	0.06	0.02	0.02		0.71	0.73	0.75	0.66	0.72	0.73
Ne	0.01	0.01	0.01	0.01	0.05	0.03	0.00	0.01	0.01		0.91	0.91	0.81	0.98	0.96
Ust	0.01	0.01	0.01	0.01	0.05	0.02	0.00	0.01	0.01	0.00		0.99	0.82	0.93	0.93
St	0.01	0.01	0.01	0.02	0.04	0.02	0.01	0.02	0.01	0.01	0.00		0.84	0.94	0.94
Rt	0.00	0.01	0.01	0.01	0.03	0.03	0.01	0.02	0.00	0.00	0.00	0.00		0.83	0.92
SB	0.01	0.01	0.01	0.01	0.04	0.02	0.01	0.02	0.00	0.01	0.00	0.00	0.00		0.98
Tbio	0.01	0.01	0.01	0.00	0.00	0.05	0.17	0.28	0.01	0.01	0.02	0.04	0.02	0.03	

[a]See table 1.1 for description of traits.

Table 1.14 Spearman family rank correlations between greenhouse seedling traits and 15-year field tree height and diameter of the same families before and after adjustment for seed weight (significant level of correlation is in the bracket) [a].

Trait	Correlations with field tree height		Correlation with field tree diameter	
	before adjustment	after adjustment	before adjustment	after adjustment
H0	0.47 (0.02)	0.38 (0.06)	0.45 (0.02)	0.33 (0.11)
H1	0.69 (0.00)	0.62 (0.00)	0.66 (0.00)	0.55 (0.00)
H2	0.67 (0.00)	0.58 (0.00)	0.60 (0.00)	0.44 (0.03)
H3	0.74 (0.00)	0.70 (0.00)	0.65 (0.00)	0.56 (0.00)
H4	0.74 (0.00)	0.68 (0.00)	0.64 (0.00)	0.54 (0.01)
NH1-0	0.72 (0.00)	0.67 (0.00)	0.69 (0.00)	0.57 (0.00)
NH2-0	0.65 (0.00)	0.62 (0.00)	0.57 (0.00)	0.49 (0.01)
NH3-0	0.73 (0.00)	0.67 (0.00)	0.63 (0.00)	0.55 (0.00)
NH4-0	0.72 (0.00)	0.66 (0.00)	0.63 (0.00)	0.53 (0.01)
D1	0.54 (0.01)	0.37 (0.07)	0.50 (0.01)	0.39 (0.06)
D2	0.60 (0.00)	0.48 (0.02)	0.54 (0.01)	0.45 (0.03)
D3	0.65 (0.00)	0.59 (0.00)	0.57 (0.00)	0.54 (0.01)
Ne	0.63 (0.00)	0.55 (0.00)	0.54 (0.01)	0.40 (0.05)
Ust	0.66 (0.00)	0.63 (0.00)	0.56 (0.00)	0.51 (0.01)
Lst	0.66 (0.00)	0.55 (0.00)	0.59 (0.00)	0.46 (0.02)
St	0.67 (0.00)	0.60 (0.00)	0.58 (0.00)	0.48 (0.02)
Rt	0.67 (0.00)	0.62 (0.00)	0.59 (0.00)	0.50 (0.01)
Br	0.44 (0.03)	0.30 (0.15)	0.36 (0.08)	0.33 (0.11)
SB	0.63 (0.00)	0.57 (0.00)	0.53 (0.01)	0.42 (0.04)
Tbio	0.65 (0.00)	0.56 (0.00)	0.56 (0.00)	0.40 (0.05)

[a] See table 1.1 for description of traits.

Table 1.15 Seedling xylem water potential (bar) under different nutrient and water treatment conditions prior to harvesting

	W1	W3	MEAN
N1	10.54 ± 3.66 n*=25	8.92 ± 1.05 n=25	9.73 ± 2.79 n=50
N2	18.86 ± 5.17 n=23	9.56 ± 1.90 n=25	14.21 ± 6.04 n=48
MEAN	14.37 ± 6.05 n=48	9.22 ± 1.54 n=50	

*n stands for the number of seedling measured.

W1 and W3 stand for, respectively, the water treatment level 1(watering once every two weeks) and water treatment level 3 (watering twice a week).

N1 and N2 are nutrient treatment level 1 (20 ppm) and nutrient treatment level 2 (200 ppm) respectively.

Table 1.16 Variance component estimates without consideration of family class effect (percent accounted for the total phenotypic variance is in the bracket)[a]

TRAIT	SOURCE				
	F	N*F	W*F	N*W*F	ERROR
H0	1.7503 (16.70)**	0.1376 (1.31)	0	0	8.5952 (81.99)
H1	9.7023 (14.66)**	1.3410 (2.03)	0.2245 (0.34)	0	54.9294 (82.98)
H2	22.8546 (21.47)**	2.6153 (2.45)*	0	0.7172 (0.67)	80.2455 (75.40)
H3	36.7982 (20.70)**	4.4620 (2.51)*	0.4520 (0.25)	0	136.0869 (76.54)
H4	37.1380 (20.34)**	3.0665 (1.68)	0	1.7717 (0.97)	140.5817 (77.01)
NH2-0	15.7613 (18.31)**	2.4473 (2.84)*	0	0.3910 (0.45)	67.5020 (78.40)
NH3-0	28.0849 (18.18)**	4.0054 (2.59)*	0	0	122.3643 (79.22)
NH4-0	28.7425 (17.92)**	2.8962 (1.68)	0	1.0451 (0.65)	127.7037 (79.62)
NH3-2	2.9940 (11.89)**	0.5639 (2.24)*	0.0687 (0.27)	0	21.5602 (85.60)
NH4-2	3.1376 (11.25)**	0.2500 (0.90)	0	0	24.4954 (87.85)
D1	6.68×10^{-3} (12.50)**	8.62×10^{-4} (1.61)	0	1.33×10^{-3} (2.50)	0.0445 (83.39)
D2	1.11×10^{-2} (11.03)*	2.63×10^{-3} (2.62)	0	2.22×10^{-3} (2.21)	0.0845 (84.14)
D3	0.0174 (9.36)**	4.99×10^{-3} (2.70)	0	0.008334 (4.49)*	0.1551 (83.47)
ND2-1	6.38×10^{-4} (2.67)	8.90×10^{-4} (3.72)**	0	0	0.0224 (93.61)
ND3-1	3.12×10^{-3} (4.08)	2.90×10^{-3} (3.79)*	0	2.51×10^{-3} (3.28)	0.0680 (88.86)
ND3-2	8.30×10^{-4} (2.06)	6.70×10^{-4} (1.66)	0	1.72×10^{-3} (4.26)*	0.03712 (91.99)
Ne	0.01869 (10.35)*	0.01036 (5.74)**	0.0010 (0.54)	1.053×10^{-3} (0.58)	0.1494 (82.79)
Ust	1.77×10^{-4} (6.94)*	1.16×10^{-4} (4.53)*	0	5.82×10^{-4} (2.28)	0.00221 (86.25)
Lst	3.78×10^{-5} (8.62)**	2.08×10^{-5} (4.74)**	0	0.43×10^{-5} (0.98)	0.00337 (85.66)
St	3.69×10^{-4} (7.87)**	2.14×10^{-4} (4.56)**	0	1.04×10^{-4} (2.21)	0.00400 (85.36)
Rt	8.75×10^{-3} (7.81)**	1.73×10^{-3} (1.55)	0	7.33×10^{-4} (0.65)	0.09901 (88.43)
Br	6.61×10^{-4} (1.99)	2.62×10^{-3} (7.88)**	4.28×10^{-4} (1.29)	1.54×10^{-4} (0.46)	0.0294 (88.39)
SB	0.0317 (8.27)*	0.0268 (6.99)**	3.45×10^{-3} (0.9)	0.76×10^{-3} (0.20)	0.3208 (83.65)
Tbio	0.0417 (5.08)**	0.0353 (4.30)**	0	6.27×10^{-3} (0.76)	0.7381 (89.86)
S/R	6.19×10^{-3} (0.71)	0.0151 (1.74)	0.0003 (.003)	0	0.8465 (97.51)
H/D	2.6650 (7.00)**	1.8603 (4.89)**	0.5054 (1.33)	0	33.0020 (86.77)
LGP	6.5215 (11.79)**	1.3690 (2.48)*	0	0.3161 (0.57)	47.1028 (85.16)

[a] See table 1.1 for description of traits.

F, N*F, W*F N*W*F and ERROR stand for variation source of family, nutrient treatment-by-family,

Table 1.17 Family rank changes between two nutrient levels in seedling total height and total dry biomass growth

FAMILY CODE	HEIGHT (H4)				TOTAL DRY BIOMASS			
	N1		N2		N1		N2	
	Mean	Rank	Mean	Rank	Mean	Rank	Mean	Rank
446	54.79	1	61.69	6	1.1104	2	2.1140	8
343	50.17	2	67.21	1	1.1946	1	2.4614	3
546	49.13	3	61.17	7	1.0583	4	2.3481	4
354	47.77	4	66.93	2	1.1004	3	2.5582	1
414	47.27	5	66.80	3	1.0271	5	2.5213	2
421	46.40	6	59.18	8	1.0001	6	2.3154	6
353	45.45	7	61.79	5	0.9810	7	1.9965	12
544	44.83	8	56.58	9	0.9427	9	2.0376	9
362	43.83	9	56.03	10	0.9297	11	2.3357	5
233	43.63	10	62.14	4	0.9718	8	2.0249	10
452	43.33	11	51.56	16	0.7922	15	1.5132	19
216	42.83	12	55.45	11	0.9350	10	1.8084	15
255	42.83	12	50.96	18	0.8209	14	1.2790	20
655	41.70	13	55.03	12	0.9100	12	1.6071	18
456	39.72	14	54.48	13	0.7695	16	2.2955	7
166	38.66	15	54.32	14	0.8539	13	2.0127	11
313	38.31	16	51.10	17	0.7164	18	1.6574	17
256	37.97	17	48.64	21	0.6618	22	1.2198	21
632	37.14	18	43.40	23	0.6819	19	1.1547	22
324	37.00	19	51.70	15	0.6807	20	1.9894	13
212	36.53	20	50.80	19	0.7364	17	1.8126	14
215	35.80	21	50.73	20	0.6806	21	1.6944	16
533	35.45	22	44.95	22	0.5343	24	1.0976	23
152	34.89	23	40.63	24	0.4961	25	0.8345	25
514	32.52	24	38.58	25	0.5805	23	1.0366	24

CHAPTER 2 PREDICTING 15-YEAR FIELD FAMILY PERFORMANCE WITH GREENHOUSE SEEDLING TRAITS

2.1 Introduction

Reliable prediction of mature tree growth with early traits can substantially shorten the long breeding cycle in most temperate tree breeding programs and can also increase the efficiency of breeding by reducing the cost of field tests. For species like jack pine (*Pinus banksiana* Lamb.), which can now accelerate flowering as early as 2-3 years from germination (Cecich et al. 1994), genetic gain from tree breeding would be greatly increased per unit time if reliable selection could be made at an early age.

Indirect early selection for mature performance in forest trees would require an early trait that is highly heritable and highly correlated, genetically, with mature tree performance (Lambeth 1980; Falconer 1981; Jiang 1985) or has the potential to correctly identify superior or inferior genotypes in the field (Carter et al. 1990). For a number of early tests conducted in several species during the past few decades, mixed results were reported on the strength of early-mature correlation and the type of early testing environment to use for increasing the early-mature correlation. For instance, while several studies suggested early-mature correlation was weak so that early performance could not reliably predict late field performance (La Farge 1975, Namkoong and Conkle 1976), others have obtained good early-late correlations or have correctly identified field growth with early traits (Squillace and Gansel 1974; Robinson and van Buijtenen 1979; Waxler and van Buijtenen 1981; Magnussen and Yeatman 1986; Riemenschneider 1988; Carter et al. 1990; and Lascoux 1993). Several studies have indicated that optimal or growth accelerating early testing conditions could promote early-mature correlations (Carter et al. 1990; Lascoux 1993). Yet, other studies have found that early testing environment that mimicked field conditions also could promote early-mature correlation prediction (Cannell 1978; Li et al. 1991).

Greenwood and Volkaert (1992) indicated that three factors could contribute to the unexplained variation after an early-mature regression. They are: (*i*) experimental error, *(ii)* rank changes due to maturation-related changes in growth behaviour, and (*iii*) G x E interaction. Among these three factors, experimental error could be reduced with large sample size, a more uniform testing environment and efficient experimental design. However, the extent of maturation-related changes in growth behaviour and the degree of G x E interaction may be specific to the species, population, or associated characteristics. For example, seasonal shoot growth pattern of 1-2 year-old jack pine seedlings was found to be different from that of most north-temperate pine species (Kremer and Larson 1982) and different responses to water stress and inconsistent early testing results were reported among seed sources of loblolly pine (Cannell 1978; Williams (1987); Li et al (1992); Waxler and van Buijtenen 1981). Therefore, an appropriate early trait and/or early testing environment for one species or population may not necessarily be applicable to other species and/or to a different set of environments. For a given species or population, if maturation-related changes plays a major role in weakening early-mature correlation, then optimal or growth accelerating conditions that promote the ontogenic development may improve early-mature correlation. On the other hand, if G x E interaction is the major cause of lowering early-mature correlation, mimicking the field conditions may have the potential to increase early-mature correlation.

In this study, I report the early testing results of jack pine in Saskatchewan, Canada. My specific objectives were: (1) to study early-late correlations between first-year jack pine seedlings growing under different nutrient and water conditions in the greenhouse and 15-year jack pines of the same families growing in the field; 2) to search for desirable early traits that are highly heritable and highly correlated to late field performance; and 3) to compare the efficiency of indirect early selection with that of direct mature selection.

2.2 Materials and methods

2.2.1 Jack pine family performance in the field in Saskatchewan

Field family tests of jack pine were established at 4 locations (table 2.1) in the western breeding district, Saskatchewan, by the Canadian Forest Service at the Northern Forest Research Centre in Edmonton. Field experimental design across four locations was a cubic lattice design which included 216 families. At each site, there were 3 replications each containing 36 incomplete block, and each incomplete block with six 4-tree row plots. For the 25 families sampled from the field experiment for a retrospective early genetic evaluation study, tree height (at age 1, 5, 10 and 15) and diameter (at age 10 and 15) were analyzed across sites using model:

$$Y_{ijkm} = u + S_i + R_{j(i)} + F_k + SF_{ik} + RF_{jk(i)} + e_{ijkm} \qquad (2.1)$$

where y_{ijkm}= measurement of the *m*th tree of the *k*th family in the *j*th replication within of the *i*th site,

u = grand mean,

S_i = effect of the *i*th site,

$R_{j(i)}$ = effect of the *j*th replication within the *i*th site,

F_k = effect of the *k*th family,

SF_{ik} = effect of *i*th site by *k*th family interaction,

$RF_{jk(i)}$= effect of *j*th replication within *i*th site by *k*th family interaction,

e_{ijkm} = residual error..

Effects of site, replication and family were all considered random. Assuming open-pollinated family variance estimates one-fourth of the additive genetic variance (Yeh and Rasmussen 1985, Wu 1993), family (h_f^2) and individual (h_i^2) heritability were estimated with the formula:

$$h_f^2 = \frac{\sigma_f^2}{\sigma_f^2 + \frac{k_{11}\sigma_{f*s}^2}{k_9} + \frac{k_{12}\sigma_{f*r(s)}^2}{k_9} + \frac{\sigma_e^2}{k_9}} \qquad (2.2),$$

$$h_i^2 = \frac{4\sigma_f^2}{\sigma_f^2 + \sigma_{f*s}^2 + \sigma_{f*r(s)}^2 + \sigma_e^2} \qquad (2.3)$$

The definitions of σ_f^2, σ_{f*s}^2, σ_{f*r}^2, $\sigma_{f*r(s)}^2$, σ_e^2 and k_1 - k_{12} were, respectively, family variance component, family-by-site interaction variance component, family-by-replication interaction variance component, family-by-replication within site interaction variance component, error term variance and their associated coefficients. The appropriate variance components were partitioned according to their Type III expected mean square (table 2.2).

Genetic correlations (r_g) of different traits measured on the same tree and the same trait measured at two different ages were estimated using the method of Falconer (1981) as:

$$r_g = \frac{cov_g(1,2)}{\sqrt{\sigma_{g1}^2 \sigma_{g2}^2}} \qquad (2.4)$$

where cov_g (1, 2) is the genetic covariance between trait 1 and trait 2; σ_{g1}^2 and σ_{g2}^2 are respectively the genetic variance of trait 1 and trait 2.

Genetic correlation between the same trait measured at different sites (type B genetic correlation) was calculated following Yamada (1962) :

$$r_g = \frac{\sigma_f^2}{\sigma_f^2 + \sigma_{fs}^2 - \frac{(\sigma_{f1} - \sigma_{f2})^2}{2}} \qquad (2.5)$$

where σ^2_f is the family variance component estimate in the combined analysis of two sites; σ^2_{fs} is the variance component estimate for family-by-site interaction in the combined analysis of two sites; σ^2_{f1} and σ^2_{f2} are the family variance component estimates at site 1 and 2 respectively. Both type B genetic correlation and regression coefficient (Bi) (Freeman 1973) in the join regression analysis were used to evaluate field family stability.

2.2.2 Predicting family performance in the field with greenhouse traits

Three methods were used to evaluate the predictability of greenhouse trait(s) to the field performance. They were: (1) Type B genetic correlation between greenhouse seedling traits observed under different nutrient and water conditions and field growth of the same families at different ages; (2) Spearman family rank correlations between greenhouse seedling traits and field growth and (3) the percentage of correct identification of the fast-growing and the slow-growing field family classes with seedling traits.

Type B genetic correlations were estimated following the approach of Yamada (1962), using formula:

$$r_g=\frac{\sigma_f^2}{\sigma_f^2+\sigma_{f*env.}^2-\frac{(\sigma_{f1}-\sigma_{f2})^2}{2}} \qquad (2.6)$$

where σ^2_f is the variance component estimate for family from the joint analysis of greenhouse and field data.

$\sigma^2_{f*env.}$ is the variance component estimated for family x environment (greenhouse or field) interaction,

σ^2_{f1} is the variance component estimated for family in environment 1 (greenhouse), and

σ^2_{f2} is the variance component estimated for family in the environment 2 (field).

Analyses of variance for greenhouse traits under each combination of nutrient treatment (2 levels) and water treatment (3 levels) levels and for field trait observed at individual site at each plantation age were performed with the model:

$$y_{ij} = u + F_i + e_{ij} \qquad (2.7)$$

where y_{ij} = the *j*th measurement in the *i*th family,

u = experiment mean,

F_i = effect of the *i*th family,

e_{ij} = experiment error.

The model used for the joint analysis of greenhouse and field data was:

$$Y_{ijk} = u + En_i + F_j + En^*F_{ij} + e_{ijk} \qquad (2.8)$$

Where Y_{ijk} = the *k*th measurements in the *j*th family in the *i*th environment,

u = experiment mean,

En_i = effect of the *i*th environment (i= 1, 2) (we considered greenhouse and field as two environments)..

F_j = effect of the *j*th family (j=1, 2, 3 ... 25),

En^*F_{ij} = effect of interaction between *i*th environment and *j*th family,

e_{ijk} = error .

In a preliminary analysis, G x E interaction in the field was found not significant, and so was family x water treatment interaction in the greenhouse seedling (chapter 1 of this thesis), type B genetic correlation between seedling traits growing in each nutrient level and the field growth trait over 4 sites was obtained using the following model for the combined analysis:

$$Y_{ijkl} = u + En_i + S_{j(i)} + F_k + En{*}F_{ik} + SF_{jk(i)} + e_{ijkl} \qquad (2.9)$$

Where Y_{ijkl}= the *l*th measurements in the *k*th family in the *j*th site (or water treatment level) within the *i*th environment,

u = ground mean,

En_i = the effect of *i*th environment (i=1 and 2, i.e. greenhouse and the field),

$S_{j(i)}$ = the effect of *j*th site (or water treatment level) within the *i*th environment,

F_k = the effect of *k*th familily,

$En{*}F_{ik}$ = the effect of interaction between the *i*th environment and the *k*th family,

$SF_{jk(i)}$= the effect of interaction between the *j*th site (or water treatment level) within the *i*th environment,

E_{ijkl} = error term.

Homogenous genetic and error variances are assumptions to obtain unbiased type B genetic correlation with unbalanced experiment data (Wu, 1993). Data of greenhouse seedlings and of field tree height measurements were standardized in this study prior to ANOVA to eliminate their differences in measuring unit so that the above two conditions could be more satisfied. The ANOVAs were then performed using SAS procedure Varcomp (SAS Inc. 1985) by considering all effects as random and variance components were partitioned in accordance with their Type I expected mean square.

To obtain Spearman family rank correlations, family means under each treatment combinations in the greenhouse and at each individual site were calculated and family rank were determined. Spearman family rank correlations between the greenhouse and field traits were obtained using SAS procedure Corr (SAS Inc. 1985).

The method used to account for the percentage of correct identification of field family rank with greenhouse traits followed the approach of Carter et al. (1990). The 25 families in the field were firstly classified as faster-growing (the top 8 families), average-growing (the middle 9 families) and slow-growing (the bottom 8 families) family classes according to their field rank. Seedling ranks were checked as yes if they fell into the right field family class, otherwise a mis-identification was recorded. If a family from the fast- or slow-growing field class fell into the slow-growing or fast-growing greenhouse classes respectively, a serious mis-identification would be recorded. The percentage of correct and mis-identification, thus, were determined by their corresponding record number in each field family class divided by the total number of families in that class. The rate of serious mis-identification was determined as the ratio of the number of serious mis-identification to the total number of families.

2.3 Results

2.3.1 Family performance in the field

Tree survival rate for the 25 families varied from 77% to 95% across the four field sites. Mean height growth across the four field plantations ranged from 3.56 to 5.35 m at age 15 (table 2.3). The considerable variation among sites in survival rate and growth was due to the large differences among sites in site quality and the degree that each site had been subject to disease infection (mainly by Western gall rust).

Family differences were significant when data were analyzed jointly across sites or for individual site. For tree height, family variance estimates accounted for 20.87%, 12.52%, 17.97% and 18.54% respectively of the total phenotypic variance at plantation age of 1, 5, 10 and 15 years (table 2.4). The absolute value of family variance estimates increased with plantation age, but the percent it accounted for total variation decreased during the period between plantation age 1 and 5 years. It then increased slightly and stabilized around 18%. For height and diameter, 62.18 -77.04% of phenotypic variation was retained among individual trees within family after age 5, which was similar to values reported in other studies (Yeh and Rasmussen 1985; Wu 1993). Family heritability estimates ranged from 0.77±0.01

to 0.84±0.01 for tree height and from 0.79±0.01 to 0.82±0.01 for diameter over ages (table 2.4). The high heritability estimates were consistent with the significant family differences detected in the ANOVAs over time.

Family-by-site interaction was not significant for tree height and diameter at all ages (table 2.4). The variance component estimates for family x site interaction accounted for less than 3% of the total phenotypic variance after age 5. However, family-by-replication within site interactions were significant at the probability level of 0.01 for height and diameter growth at all ages. The percent that family x replication/site interaction accounted for the total phenotypic variation was comparable to that of family, being 12-18% of total phenotypic variance after age 5.

Highly stable family performances across sites were confirmed by type B genetic correlations estimates and Spearman family rank correlations (table 2.5). Checking the mean growth of each family, it was found that the eight top- and bottom-ranking families did not change their ranks very much relative to the other families across sites, although there were some rank changes among themselves (table 2.6). Joint regression coefficients (Bi) indicated that the fast-growing families generally had greater response to site quality (indicated by the average growth of all families) and Bi was significantly correlated with family mean growth (table 2.7).

Genetic correlations for tree height and diameter measured at age 1, 5, 10 and 15 years were high, ranging from 0.72 to 1.00, so were the Spearman family rank correlations (table 2.8). The strong age-age correlation indicated very stable family performance over time and relatively little mature-related change in family rank.

2.3.2 Predicting field performance with greenhouse traits

2.3.2.1 Type B genetic correlation

For a total of 1800 possible type B genetic correlations (25 seedling traits x 6 treatment combinations x 4 field sites x 3 field ages) between greenhouse traits measured under each combination of nutrient and water treatments and field traits observed at individual site at different plantation ages (5, 10 and 15 years), a wide range of r_g estimates were obtained, ranging from 0.00 to 1.00. Some of the high estimates could be biased because they were reached not because of their zero or small variance component in family-by-environment interaction but because of their large differences in family variances between the greenhouse and the field traits, resulting in the larger values of adjustment in the denominator in formula 2.6. Since homogenous family variances and homogenous error variances were assumed in order to obtain an unbiased type B genetic correlation for unbalanced data (Yamada 1962; Wu 1993), we arbitrarily neglected those estimates if they did not satisfy the above two conditions (i.e. type B genetic correlation would be biased and invalid if the variance component ratio between greenhouse and field traits in the error term or family was larger than 1.25 or 2.5). Threshold values of 1.25 and

2.5 were adopted as the approximate F values at the significant level of 0.05 with degree of freedoms of 15/15 and 200/200 respectively. As a result, about 22% of the possible type B genetic correlations were biased estimates and most of them were estimated with seedling ratio traits (such as S/R) or organ dry biomass traits.

Field tree height across four sites yielded moderate to high type B genetic correlations with greenhouse seedling traits, ranging from 0.36-0.70, 0.28-0.82 and 0.23-0.71 respectively for field age of 5- 10- and 15-year. Despite the large growth differences among the four field sites in mean height growth, there were small differences among sites in type B genetic correlation estimates (table 2.9). Small differences among four field sites in type B genetic correlation estimates were consistent with the non-significant G x E interaction detected among them in tree height and diameter growth .

Several seedling traits, including absolute height (H1, H2, H3, H4) and height increment (NH1-0, NH2-0, NH3-0, NH4-0, NH3-2 and NH4-2), later basal diameter measurement (D3), needle dry biomass (Ne), stem dry biomass (Ust, Lst), shoot dry biomass (SB) and total dy biomass (Tbio) showed good predictability of field performance. It was also apparent that seedling height and diameter measured at the larger seedling age generally gave the better prediction. Comparatively, the length of hypocotyl (H0) which was measured as the distance between soil surface and the first leaf, early basal diameter measurement (D1) and shoot/root dry biomass ratio (S/R) ratio had demonstrated relative poorer prediction of field performance (table 2.9 and 2.10).

Type B genetic correlation estimates between greenhouse traits and field height growth did not decrease with plantation age. In fact, in many cases the mean type B genetic correlation estimates between seedling traits and 15-year field height growth were higher than those estimates between seedling traits and 5-year field height growth (table 2.10).

Early testing environments showed considerable influence on type B genetic correlation estimates. Low nutrient supply coupled with moist condition (N1W3) gave persistently better prediction of field performance than any other treatment combinations (table 2.11). Furthermore, the superiority of this treatment combination to others was not site or age specific but applicable to all field sites, plantation ages and seedling traits. Low nutrient level gave a slightly higher type B genetic correlation than the high nutrient level, although high nutrient level was found to promote seedling size growth, morphological development and family differentiation (chapter 1 of this thesis).

2.3.2.2 Spearman family rank correlation

One of the important objectives of greenhouse early testing is to correctly rank the growth of families in the field with the appropriate early traits (or seedling traits). We used Spearman rank correlation as an indicator to the degree that field family rank was correctly predicted by the family rank in seedling traits. In this study, 0.40-0.69, 0.41-0.73 and 0.43-0.74 of family rank correlations were obtained respectively between 5-, 10- and 15-year field height growth and different greenhouse seedling traits (table 2.12). The four field sites differed in the magnitude and the number of significant Spearman correlations (which were significant at the probability level of 0.05) between 15-year field height and 20 different seedling traits under different treatment conditions in the greenhouse. It appeared that the higher the field site quality, as indicated by site mean tree height growth, the greater and more significant Spearman correlations between field growth and greenhouse seedling traits (table 2.12). Linear correlation existed between the number of significant Spearman correlations and site mean plantation height ($r=0.96$, Prob $>|r| = 0.04$, $n=4$).

Seedling traits differed in their abilities to give precise prediction of field family rank in height at 5- 10- and 15-year ages and the relative superiority of seedling traits was affected by the nutrient conditions under which seedlings were grown (table 2.13, 2.14). In the high nutrient level, accumulated seedling height growth increment beyond the hypocotyl yielded the highest family rank correlation with field height growth at ages of 5, 10 and 15. However, in the low nutrient level, seedling shoot dry biomass measurement (SB) produced the highest family rank correlation with field height in the three plantation ages. With age, absolute height and diameter measurements, seedling height increments beyond the hypocotyl and some seedling organ dry biomass, such as needle dry biomass, stem dry biomass, root dy biomass and total dry biomass, also gave good ($r>0.6$) early-mature family rank correlations. Contrastingly, the length of hypocotyl, shoot/root ratio (S/R) and the length of growth period gave much lower family rank correlations.

Greenhouse environments also showed considerable effects on the magnitude of spearman family rank correlations (table 2.14). Treatment combination of low nutrient and frequent watering (N1W3) frequently produced higher greenhouse-field family rank correlation at the four sites and at the three plantation ages. This corresponds to type B genetic correlation estimates. Comparing the two nutrient levels, low nutrient supply to seedlings in the growing season again yielded, on average, higher family rank correlation than the high nutrient supply for most of the traits. Furthermore, for the 20 different seedling traits measured in the low nutrient level, similar number of significant spearman correlations (45 - 53 out of 60) with 15-year field height was observed at each of the four field sites. However, for the same seedling traits measured under the high nutrient condition, there was smaller number of significant correlations (9 and 28 out of 60) at the two sites with relative poorer growth (site 4 and site 2). This contrasted with 41 and 49 (out of 60) at the two sites with relatively good growth (site 3 and 1 respectively).

2.3.2.3 Percent of correct identification of field family classes

The percent of correct identification of field family classes based on greenhouse performance varied according to the three field family classes (fast, average and slow growth), seedling traits and seedling growing conditions in the greenhouse. They averaged from 25 to 87.75%, 0 to 77.78% and 14.3 to 87.5%, respectively, for the fast-, average- and slow-growing family classes. The percent of correct identification (table 2.15) did not vary greatly for any of the field family classes among sites. However, the percent of correct identifications for the fast- and slow-growing family classes were higher than that for the average-growing family class (table 2.15). This was due to the frequent family rank changes between the fast-growing family class and the average-growing family class or between the slow-growing family class and the average-growing family classes relative to that between the fast-growing family class and the slow-growing family class.

Many seedling traits such as seedling absolute height (H1, H2, H3 and H4), seedling height increment (Nh1-0, Nh2-0, NH3-0, NH4-0 and NH3-2) and organ dry biomass (Ust, St and SB) gave good identification of field family classes (table 2.16-2.19). For such seedling traits, the percent of correctly identifying the fast-growing and the slow-growing field family classes averaged around 59% and 58% respectively.

Serious mis-classification of field family classes could be found with all seedling traits, but the low percentage suggested this should not be of serious concern (table 2.18). For all seedling traits, the average percent of serious mis-classification was less than 6 percent and there was no serious misclassification under some specific combinations of site, seedling trait and seedling growing environment.

Nutrient and water conditions in the greenhouse again showed significant influence on the percent of correct identification. The averaged percent of correct identification for the fast- and slow-growing family classes was slightly higher in the low nutrient level (table 2.14, 2.18 and 2,19), especially under treatment combination of N1W3, than in the high nutrient level. However, the percent of serious mis-classification did not show such trend.

2.4 Discussion

2.4.1 Family performance in field genetic tests

Field plantation at the best site (site 3) was 50% higher (60% larger in diameter) than that at the worst site (site 4). This reflected the considerable differences in site quality among the four field locations. Large variation in site quality is not surprising since the four sites were purposely chosen with different physiographic or soil conditions to represent the available forest lands in the breeding district (Klein 1982). Phenotypic variation coefficient among four sites ranged from 7.57-8.25% in tree height at age 15. The similar degree of phenotypic variation could be the result of the same set of testing materials and the similar responses of genotypes to changed environment. However, the average phenotypic variation of four sites decreased from 15.38% at age 5 to 8.06% at age 15 (table 2.3). This sharp decrease could be the result of faster tree height growth relative to the increase of variation among trees. It could also be caused by the stronger effect of environment on tree height growth with the increase of age.

The highly significant differences detected among families were not unexpected since this sample of jack pine included many top-ranking and bottom-ranking families. If a more random sample were drawn from the 216 families, genetic differences among families might be less. However, in a genetic analysis of the 216 families (Klein 1982) at age 5, significant variation among families was also observed at the 99% confidence level. Thus, although family differences in this sample might have been inflated by the sampling method, they at least partially reflected the large genetic variation in this breeding population. One possible reason in observing such larger genetic variation among families was probably due to the fact that during the selection of trees in the wild, little emphasis was given to their growth rate (Klein 1982). Therefore, genetic variation of growth in the natural stands did not dramatically reduce as a result of selection.

Individual and family heritability estimates for tree height and diameter from this sub-sample were considerably greater than those estimates in some studies of this species (Riemenschneider 1988 and Morris et al. 1991). However, they were close to the value obtained by others (Adams et al. 1991) at similar age. Since heritability is a parameter associated with a given population and its environment, the large differences among studies do not invalidate one or the other. In our case, the heritability estimates might have be inflated by the sampling method as mentioned above, by the effects of provenance and stand (Jeffers and Jensen 1980), and by the possible inbred or self-fertilized seeds (Cheliak et al. 1985), they, therefore, could be regarded as possible upper limits of the whole population.

Although family-by-replication interaction was significant when data from the four sites were analyzed by individual site or jointly, family-by-site interaction was negligible at all ages for height and diameter growth. Variance component estimates for family-by-site interaction accounted for less than 3% of total phenotypic variance and were less than one-ninth of those for family after age 5. However, variance component estimates for family-by-replication interaction accounted for 14-17.2% of total phenotypic variance, which were only slightly smaller than those for family. This result might reflect the relatively homogeneous environmental conditions within a replication and heterogeneous environmental conditions among replications within a site. This situation was less expected since the effect of block was ignored from its original BIB (balanced incomplete block) experimental design during the data analyses, random variation within a replication, thus, might have chance to be larger (Cochran and Cox 1968). Whether the real field experimental array supports the above reasoning will not be known until detailed field information is available.

The insignificant family x site interaction suggested the high stability of family performance. This was confirmed by type B genetic correlations and Spearman family rank correlations for height growth observed among sites. Thus, the weak family x site interaction might be due to the relatively high family stability, small differences in site quality that induce different family responses and large genetic differences among families. However, since site quality were quite different among site as indicated by the average growth of tree height (table 2.3), it is less likely to be an important factor. Thus, the lack of significant G x E interaction could be mainly attributed to the large family differences and high family stabilities. Insignificant G x E interactions have been previously reported in jack pine (Greenwood 1992).

Results of field genetic tests have several implications to jack pine tree breeding program in Saskatchewan. First, due to the insignificant site x family interaction, superior families selected at one site will also be expected to be superior at another site despite their possible large differences in site quality. Consequently, there is no need to subdivide the breeding population since a common set of families could serve the breeding requirements in the breeding district. Second, due to the considerable large genetic variation in the base breeding population (Klein 1982) and the high family heritability estimates, great genetic gain would be expected by mature direct family selection alone. Third, in this study, high age-age correlations were found and they were very close to unity after age 5. This might well suggest that selection in jack pine can be made at an early age. In doing so, the cost associated with progeny test, including maintenance, and continuous monitoring could be reduced greatly in jack pine.

2.4.2 Predicting 15-year field height growth with greenhouse traits

High predictability of late field family performance with 6-months seedling traits in this study confirmed the possibility of making early indirect selection for field performance in jack pine and corroborated the results of other studies with Eastern populations of this species (Magnussen and Yeatman 1986; Riemenschneider 1988; Carter et al. 1990). It seemed that precise prediction of late field family performance could be achieved at a very early stage in jack pine. In this study, although the sampling of field performing classes might have inflated the greenhouse-field correlations, a considerable prediction was actually achieved even as early as two months of seedling age (H1), and the results steadily improved with seedling ages. Riemenschneider (1990) also indicated that reliable early selection in jack pine was possible at ages one to two years.

It is interesting that while weak correlations between early and late performance were frequently reported in several conifer species, consistently high and positive correlations were found in jack pine. This might be an unique feature of this specie. It might also suggest that early-mature correlation is species specific, and a single trend may not be applicable to all pine species. Another interesting phenomena in jack pine is that ovulate flower can be obtained in two years, which is rare for many other pine species (Cecich et al. 1994). Since the onset of flowering is a readily indication of juvenile-mature phase change (Zimmerman 1972), early flowering in jack pine might imply that its seedling would be biologically more mature than some other pines of similar age and that its early and mature traits would be more controlled by a common set of genes.

In agreement with previous findings, absolute seedling height and accumulated height increment beyond the hypocotyl demonstrated their good predictability of family performance in the field. Since these greenhouse seedling traits also had the highest estimates of heritability (chapter 1 of this thesis) which are important parameters for indirect selection, there is no doubt that they should be the target greenhouse traits in jack pine for early selection. Height increment between two to six months of seedling growth gave even better prediction of field performance (table 2.9-2.11), which was consistent with numerous reports that late seedling height increment in the greenhouse gave best prediction of field performance (Carter et al. 1990; Williams 1987).

Besides height and height increment, seedling organ dry biomass and total dry biomass also showed high greenhouse-field correlations and good predictability of field family classes. This paralleled the high genetic correlations among seedling traits. However, relative to seedling height and height increment, these seedling traits generally had lower family heritability, therefore, would be less efficient in early indirect selection than seedling height or height increment.

Early seedling basal diameter gave relative poor prediction of field family performance. Although the predictability of basal diameter was improved with age, it did not show as good predictability of field performance as traits of seedling height or organ dry biomass. Basal diameter increments (ND3-1 and ND3-2) occasionally gave good prediction of field performance, but their heritability estimates were considerably lower mainly due to the relatively large measurement error. The potential of these traits for use in an early selection would also be limited.

Shoot/root ratio (S/R) could not be a good early traits in predicting field performance in jack pine, although this trait gave the best prediction of field performance in loblolly pine (Waxler and van Buijtenen 1981) and lodgepole pine (Wu, 1993). In this study, S/R varied insignificantly among the three field family classes (chapter 1 of this thesis), thus, was not discriminative to the largest genetic differences in the field. In this study, it was also found that seedling S/R had the most heterogeneous family and error variances with that of 5-, 10- and 15-year field height even after data standardization. More than 80% of possible type B genetic correlation estimates between S/R and field tree height were biased as the high values were caused by the large adjustment in the denominator in formula 2.6.

The considerable effect of nutrient conditions in the greenhouse on the greenhouse-field correlations was unexpected since G x E interaction was not detected in the field and only weak family x nutrient interaction was found in the greenhouse traits. However, the higher greenhouse-field correlations achieved under low nutrient condition, especially under the treatment combination of N1W3, indicated that nutrient conditions did make a difference in early testing of jack pine. Some possible reasons for this result could be: (*i*) low nutrient in greenhouse simulated the low nutrient availability in the field where jack pine progeny plantations were established, (*ii*) seedling competitions in the greenhouse in the high nutrient level and (*iii*) sampling error.

Nutrient availability in the field was probably low since almost all the progeny plantations were established on sand or sandy soil (Klein 1982). Sandy soil is usually characterized as having poor nutrient retaining ability and good draining property. In Saskatchewan and Manitoba, nutrient deficiency on sites with sand or sandy soil had been identified as a limiting factor to tree growth (Zoltai et al. 1970). If poor nutrient condition in the field was the real reason which resulted in better greenhouse-field correlation under low nutrient treatment, it confirms the assumption that similar nutrient condition promotes similar gene(s) expression in jack pine and mimicking field condition will improve early-mature correlation (Cannell et al. 1978; Li et al. 1992).

Competition between seedlings growing in the high nutrient level could be another reason that decrease the greenhouse-field correlations. Because seedlings grew much faster under the high nutrient condition and their canopy closed earlier than those in the low nutrient level, intense seedling competition for light and growing space was observed in the high nutrient level but not in the low nutrient level. Since jack pine is a species of low tolerance to shading, it was possible that some families with fast growth in a relative later stage might not have had the chance to fully express their growth potential.

Sampling error could be another reason that increase the greenhouse-field correlations. Trait H1 was measured prior to the application of nutrient and water treatments. If sample error was negligible, its correlation with 15-year field height would be expected to show no difference between the two nutrient levels and among the 6 treatment combinations. However, in this study, type B genetic correlations between H1 and 15-year field height were slightly higher in the low nutrient level and in the treatment combination of N1W3, although no such trend was found with the Spearman rank correlations. Therefore, sampling error could not be excluded as a possible cause.

An interesting phenomena in this study was that neither type B genetic correlation nor Spearman rank correlation between seedling traits and field tree height decreased with increasing plantation age. This is not consistent with the findings of Lambeth (1980) in Pinacae, and Riemenschneider (1988) in jack pine that juvenile-mature correlation decreased with increasing plantation ages. In this study, correlations between greenhouse traits and 15-year field tree height were actually slightly higher than the correlations between greenhouse traits and 5-year field tree height. This could be caused by the persistently large family differences in the greenhouse and in the field, or it could be caused by random effects.

Despite the fluctuation of greenhouse-field correlations estimated among different early testing conditions, the pooled value was still high enough to justify an early selection in jack pine. Lambeth (1980) and Jiang (1985) indicated that the relative efficiency of early selection (RSE) could be computed with the following formula:

$$RSE = G_j T_m / G_m T_j$$

$$= r_{g(j.m)} I_j h_j T_m / I_m h_m T_j$$

where G = genetic gain,

r_g = genetic correlation between juvenile and mature trait(s),

I = selection intensity,

h = square root of heritability,

T = number of years required to complete a breeding cycle,

m = mature trait(s),

J = juvenile trait(s).

We assume the selection intensities in 1-year seedlings and in 15-year planation are the same and 5 and 3 years beyond the end of progeny testing will be needed to complete a breeding cycle for the greenhouse and field population respectively. The relative efficiency for indirect selection of 15-year field height with 1-year seedling traits is more than twice that for direct selection at plantation age 15 years (table 2.21).

2.5 Literature cited

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Table 2.1 **Description of site conditions of the four field progeny tests in Saskatchewan (Klein 1982)**

Characteristics	Site 1	Site 2	Site 3	Site 4
LOCATION				
Province	Saskatchewan			
Town	Snowden		Glaslyn	
N latitude	53°51'	53°52'	53°39'	53°46'
W longitude	104°38'	104°38'	108°19'	108°22'
Elevation, m	510	510	755	670
Township-range	56-18	56-18	54-16	55-17
PHYSIOGRAPHY				
Physiographic area	Lower Torch River Plain		Thickwood Hills	
Surface deposit	Glacio-fluvial		Ground moraine	
SOIL				
Subgroup	Eluviated Eutric Brunisol		Orthic Gray Luvisol	
Dominant texture	Sand	Loamy sand	Sandy clay loam	
Estimated drainage	Rapidly drained		Moderately well drained	
Association	Kewanoke		Loon River	
CLIMATE				
Mean temp., °C				
July	16	16	18	18
January	-20	-20	-19	-19
Degree-days above 5°C	1100	1100	1050	1050
Frost-free period, 0°C days	70	70	70	70
Mean precip., mm				
Annual	420	420	400	400
May-Sept.	280	280	260	260

Table 2.2 Expected mean sqaure in analyses of variance (ANOVA) for field data of combined sites.

Source	df	Expected mean square for combined sites
Site (S)	3	$\sigma_{e}^{2} + k_{1}\sigma_{f*r(s)}^{2} + k_{2}\sigma_{s*f}^{2} + k_{3}\sigma_{r(s)}^{2} + k_{4}\sigma_{s}^{2}$
Rep./Site (R/S)	8	$\sigma_{e}^{2} + k_{5}\sigma_{f*r(s)}^{2} + k_{6}\sigma_{r(s)}^{2}$
Family (F)	24	$\sigma_{e}^{2} + k_{7}\sigma_{f*r(s)}^{2} + k_{8}\sigma_{s*f}^{2} + k_{9}\sigma_{f}^{2}$
S x F	72	$\sigma_{e}^{2} + k_{10}\sigma_{f*r(s)}^{2} + k_{11}\sigma_{s*f}^{2}$
R/S x F	192	$\sigma_{e}^{2} + k_{12}\sigma_{f*r(s)}^{2}$
Error	1203	σ_{e}^{2}

Note: σ_{s}^{2}, $\sigma_{r(s)}^{2}$, σ_{f}^{2}, σ_{s*f}^{2}, $\sigma_{f*r(s)}^{2}$ and σ_{e}^{2} are variance components of site (S), replication within site (R/S), family (F), site-by-family interaction (S x F), replication within site-by-family interaction (R/S x F) and error term respectively.
k_i is the coefficient of variance components with $k_1=3.176$, $k_2=9.529$, $k_3=79.408$, $k_4=238.23$, $k_5=3.206$, $k_6=80.143$, $k_7=3.154$, $k_8=9.462$, $k_9=37.849$, $k_{10}=3.237$, $k_{11}=9.711$ and $k_{12}=3.349$.

Table 2.3 **Mean height (cm) and diameter (cm) growth of 25 open-pollinated jack pine families in the field progeny tests in Saskatchewan**

Trait		Site 1	Site 2	Site 3	Site 4	sites combined
H0	mean	11.45	10.00	6.49	6.77	8.50
	c.v. (%)	13.17	14.09	15.73	16.72	14.82
H5	mean	143.89	144.21	144.52	123.66	138.66
	c.v. (%)	17.37	14.09	15.48	14.19	15.38
H10	mean	342.09	279.54	354.01	246.42	305.24
	c.v. (%)	10.40	8.42	10.44	9.99	10.12
H15	mean	529.24	418.76	534.64	355.60	458.61
	c.v. (%)	8.25	7.57	7.83	8.11	8.06
D10	mean	47.15	39.21	48.60	29.74	41.03
	c.v. (%)	19.51	19.77	17.64	22.18	19.60
D15	mean	83.39	66.80	84.16	52.94	71.59
	c.v. (%)	15.90	16.26	13.89	17.82	15.80

Note: H0, H5, H10, H15, D10 and D15 are respectively the tree height measurements at plantation ages of 0-, 5-, 10- and 15-year and diameter measurements at plantation ages of 10- and 15-years. c.v. (%) is the coefficient of variation.

Table 2.4 Variance component (percentage in brackets) estimates for 25 open-pollinated jack pine families in the field progeny test across 4 sites

Plantation age		1	5	10	15
H	F	0.6823**	81.7480**	258.5432**	407.2022**
		(20.87)	(12.52)	(17.97)	(18.54)
	FxS	0.2140	14.7213	23.6388	45.5055
		(6.54)	(2.25)	(1.64)	(2.07)
	FxR/S	0.7886**	101.8542**	201.2880**	377.8087**
		(24.12)	(15.59)	(13.99)	(17.20)
	ERR.	1.5851	454.8747	954.9593	1365.4681
		(48.47)	(69.64)	(66.39)	(62.18)
	h_f^2	0.80±0.01	0.77±0.01	0.84±0.01	0.83±0.01
	h_i^2	0.83±0.23	0.50±0.16	0.72±0.19	0.74±0.20
D	F			12.2725**	21.9650**
				(13.14)	(13.23)
	FxS			0.2349	0.4734
				(0.25)	(0.29)
	FxR/S			16.2568**	15.6906**
				(17.40)	(9.45)
	ERR.			64.6573	127.9086
				(69.21)	(77.04)
	h_f^2			0.79±0.01	0.82±0.01
	h_i^2			0.53±0.16	0.53±0.16

Note: F, FxS, FxR/S and ERR refer to the effect of family, family-by-site interaction, family-by replication within site interaction and error respectively. H is tree height measurement and D is tree diameter measurement.

** indicates the effect is significant at the probability level of 0.01.

h_f^2 and h_i^2 are estimates of family heritability and individual heritability respectively.

Table 2.5 Type B genetic correlations(upper diagonal) and Spearman family rank correlations (lower diagonal) among four sites in tree height in Saskatchewan for 25 open-pollinated jack pine families.

	Site 1	Site 2	site 3	Site 4
site 1		0.87	0.99	1.00
site 2	0.51		0.95	1.00
site 3	0.66	0.62		0.83
site 4	0.54	0.59	0.49	

Note: all Spearman correlations are significant at the probability level of 0.001.

Table 2.6 Family mean height (cm) and rank changes across 4 sites in the field at plantation age of 15 years

Family Code	Site 1		Site 2		Site 3		Site 4	
	Mean	Rank	Mean	Rank	Mean	Rank	Mean	Rank
233	611.00	1	436.25	5	567.82	3	358.18	12
546	587.00	2	435.50	7	565.08	6	383.70	1
343	581.00	3	385.50	24	569.46	2	372.82	5
446	568.63	4	459.09	2	561.20	7	383.17	2
216	560.63	5	433.75	8	566.36	4	365.17	7
353	557.00	6	464.58	1	549.08	10	375.50	4
414	547.40	7	425.22	9	534.46	14	356.40	13
362	547.10	8	448.22	4	566.20	5	362.17	9
655	546.71	9	407.90	15	519.90	19	345.17	19
215	534.30	10	395.38	19	543.17	13	322.70	25
456	532.71	11	405.89	16	523.50	16	362.08	10
354	532.50	12	457.11	3	569.70	1	381.58	3
514	523.91	13	386.22	22	497.33	22	363.18	8
255	523.30	14	415.22	12	547.64	11	348.90	15
632	518.18	15	436.09	6	520.09	18	366.55	6
452	517.80	16	403.67	18	486.50	24	348.83	16
544	515.90	17	422.33	11	550.67	9	354.00	14
166	515.22	18	423.33	10	543.67	12	341.27	20
421	511.50	19	411.2	13	503.00	20	326.73	24
256	502.75	20	405.00	17	556.92	8	336.18	22
212	496.60	21	390.00	21	495.25	23	327.67	23
533	494.40	22	383.50	25	521.18	17	347.50	18
152	491.30	23	392.89	20	485.09	25	340.82	21
324	475.80	24	385.80	23	497.80	21	358.82	11
313	464.78	25	410.13	14	526.75	15	348.18	17

Table 2.7 **Family stabilities as indicated by the slopes in joint regression analyses (Bi) with tree height (H) and diameter (D) at the plantation ages of 10 and 15 years**

FAMILY CIASS	FAMILY CODE	Bi			
		H10	D10	H15	D15
fast-growing	233	1.3138	1.5128	1.3536	1.4680
	354	0.9388	0.5681	0.8735	0.7154
	362	1.0753	1.2172	1.1029	1.1963
	546	1.1178	0.7994	1.0165	1.0562
	353	0.9600	1.0653	0.9771	1.1730
	343	1.2520	1.2914	1.3588	1.2515
	216	1.1290	1.1854	1.2311	1.0979
	446	1.0099	0.9118	1.1541	0.9048
	mean	1.100	1.0689	1.1335	1.1079
average growing	655	1.0714	1.0848	0.9967	1.0184
	166	1.0437	0.9715	1.0544	0.9194
	544	1.0128	1.0485	0.9704	0.9800
	255	1.0611	0.7227	0.9807	0.9671
	215	1.2337	1.3148	1.2273	1.1700
	414	1.0394	1.0049	0.8768	0.9725
	456	0.9676	0.8876	0.9527	0.9749
	256	1.1048	1.2389	1.2709	1.1807
	632	0.8385	1.0352	0.8839	1.0200
	mean	1.0414	1.0343	1.0238	1.0225
slow-growing	452	0.8653	0.7250	0.8004	0.8020
	313	0.8275	0.7195	0.8284	0.9026
	324	0.7614	0.6322	0.8285	0.7330
	152	0.8358	0.8022	0.8914	0.9471
	533	0.9496	0.8838	0.9424	1.0263
	421	0.9869	1.1515	1.0046	1.0988
	514	0.8853	0.8405	0.8923	0.7862
	212	0.9497	0.9588	0.8502	0.9306
	mean	0.8827	0.8393	0.8795	0.9033

Table 2.8 **Genetic correlation (upper diagonal) and Spearman family rank correlations (lower diagonal) among height and diameter traits measured at different plantation ages (standard errors of genetic correlation and significant levels of Spearman correlation are in brackets).**

	h1	h5	h10	h15	d10	d15
h1		0.90 (0.02)	0.72 (0.04)	0.73 (0.04)	0.73 (0.04)	0.72 (0.04)
h5	0.71 (0.00)		0.98 (0.00)	0.99 (0.00)	0.99 (0.00)	1.00 (0.00)
h10	0.60 (0.00)	0.89 (0.00)		1.00 (0.00)	0.97 0.01	0.97 0.01
h15	0.63 (0.00)	0.87 (0.00)	0.96 (0.00)		0.98 (0.00)	0.99 (0.00)
d10	0.60 (0.00)	0.90 (0.00)	0.92 (0.00)	0.90 (0.00)		0.98 (0.00)
d15	0.61 (0.00)	0.89 (0.00)	0.92 (0.00)	0.92 (0.00)	0.96 (0.00)	

Note: h1, h5, h10 and h15 are respectively tree height at plantation ages of 1, 5, 10 and 15 years; d10 and d15 are tree diameter at plantation ages of 10 and 15 years.

Table 2.9 Mean type B genetic correlation estimates and their standard deviations between greenhouse jack pine seedling traits and 15-year field tree height of the same families at four sites in Saskatchewan (number in brackets indicates the number of estimates from which the mean and standard deviation were derived)[a]

Trait	Site 1	Site 2	Site 3	Site 4	combined
H0	0.29± 0.13 (5)	0.71± 0.12 (5)	0.41± 0.06 (5)	0.39± 0.20 (6)	0.45± 0.20 (21)
H1	0.59± 0.12 (6)	0.79± 0.12 (6)	0.67± 0.08 (6)	0.58± 0.14 (6)	0.59± 0.14 (24)
H2	0.63± 0.13 (6)	0.74± 0.13 (6)	0.67± 0.06 (6)	0.56± 0.12 (6)	0.65± 0.13 (24)
H3	0.76± 0.09 (6)	0.71± 0.10 (6)	0.72± 0.06 (6)	0.63± 0.10 (6)	0.70± 0.10 (24)
H4	0.75± 0.10 (6)	0.72± 0.12 (6)	0.73± 0.08 (6)	0.64± 0.09 (6)	0.71± 0.10 (24)
NH1-0	0.67± 0.12 (6)	0.77± 0.13 (6)	0.73± 0.09 (6)	0.64± 0.13 (6)	0.70± 0.12 (24)
NH2-0	0.65± 0.13 (6)	0.69± 0.13 (6)	0.70± 0.09 (6)	0.57± 0.11 (6)	0.65± 0.12 (24)
NH3-0	0.80± 0.09 (6)	0.66± 0.10 (6)	0.74± 0.08 (6)	0.64± 0.10 (6)	0.71± 0.11 (24)
NH4-0	0.78± 0.10 (6)	0.66± 0.13 (6)	0.75± 0.10 (6)	0.66± 0.10 (6)	0.71± 0.12 (24)
NH3-2	0.92± 0.06 (5)	0.47± 0.19 (5)	0.65± 0.13 (5)	0.73± 0.16 (6)	0.69± 0.21 (21)
NH4-2	0.86± 0.14 (2)	0.43± 0.33 (3)	0.66± 0.25 (3)	0.77± 0.17 (6)	0.69± 0.25 (14)
D1	0.47± 0.36 (3)	0.61± 0.21 (6)	0.53± 0.11 (6)	0.59± 0.21 (6)	0.56± 0.20 (21)
D2	0.53± 0.26 (4)	0.67± 0.18 (5)	0.61± 0.07 (5)	0.59± 0.21 (5)	0.60± 0.18 (19)
D3	0.57± 0.17 (3)	0.69± 0.24 (5)	0.67± 0.15 (6)	0.68± 0.27 (6)	0.66± 0.20 (20)
NE	0.68± 0.21 (6)	0.67± 0.16 (6)	0.72± 0.13 (6)	0.58± 0.14 (6)	0.66± 0.16 (24)
UST	0.74± 0.22 (4)	0.60± 0.24 (5)	0.71± 0.16 (5)	0.68± 0.12 (5)	0.68± 0.18 (19)
LST	0.71± 0.28 (4)	0.77± 0.23 (5)	0.70± 0.13 (6)	0.72± 0.22 (6)	0.72± 0.20 (21)
RT	—	—	—	0.57± 0.24 (3)	0.57± 0.24 (3)
SB	0.70± 0.20 (5)	0.65± 0.17 (6)	0.69± 0.15 (6)	0.62± 0.13 (6)	0.66± 0.15 (23)
TBIO	0.81± 0.14 (3)	0.67± 0.20 (5)	0.70± 0.18 (5)	0.66± 0.16 (6)	0.69± 0.17 (19)
S/R	—	—	—	0.23± 0.17 (2)	0.23± 0.17 (2)
H/D	0.61 (1)	0.40± 0.10 (2)	0.58± 0.07 (2)	0.37± 0.13 (4)	0.45± 0.14 (9)

[a] See table 1.1 for description of traits.

Table 2.10 Mean type B genetic correlation estimates and the standard deviations between greenhouse jack pine seedling traits and 5-, 10- and 15-year field tree height of the same families across four sites (number in brackets indicates the number of estimates from which the mean and standard deviation were derived)[a]

Seedling Trait	Field Plantation age (years)			
	5	10	15	combined
H0	0.36± 0.19 (24)	0.44± 0.22 (22)	0.45± 0.20 (21)	0.42± 0.20 (67)
H1	0.59± 0.15 (22)	0.67± 0.14 (24)	0.66± 0.14 (24)	0.64± 0.15 (70)
H2	0.60± 0.18 (24)	0.66± 0.12 (24)	0.65± 0.13 (24)	0.64± 0.15 (72)
H3	0.63± 0.14 (24)	0.71± 0.11 (24)	0.70± 0.09 (24)	0.68± 0.12 (72)
H4	0.63± 0.15 (24)	0.71± 0.12 (24)	0.71± 0.10 (24)	0.68± 0.13 (72)
NH1-0	0.63± 0.18 (24)	0.73± 0.13 (24)	0.70± 0.12 (24)	0.69± 0.15 (72)
NH2-0	0.64± 0.19 (24)	0.67± 0.12 (24)	0.65± 0.12 (24)	0.65± 0.14 (72)
NH3-0	0.65± 0.15 (24)	0.72± 0.11 (24)	0.71± 0.11 (24)	0.69± 0.13 (72)
NH4-0	0.66± 0.10 (24)	0.72± 0.12 (24)	0.71± 0.12 (24)	0.70± 0.14 (72)
NH3-2	0.59± 0.21 (24)	0.68± 0.19 (24)	0.69± 0.21 (24)	0.65± 0.21 (67)
NH4-2	0.64± 0.23 (24)	0.69± 0.22 (17)	0.69± 0.25 (14)	0.67± 0.23 (55)
D1	0.47± 0.24 (24)	0.53± 0.22 (22)	0.56± 0.20 (21)	0.52± 0.22 (67)
D2	0.54± 0.26 (22)	0.60± 0.20 (19)	0.60± 0.18 (19)	0.58± 0.22 (60)
D3	0.57± 0.26 (24)	0.65± 0.19 (20)	0.66± 0.20 (20)	0.62± 0.22 (64)
Ne	0.58± 0.20 (24)	0.67± 0.16 (24)	0.66± 0.16 (24)	0.64± 0.18 (72)
UST	0.65± 0.26 (22)	0.68± 0.20 (19)	0.68± 0.18 (19)	0.67± 0.21 (60)
LST	0.58± 0.25 (24)	0.70± 0.20 (21)	0.72± 0.20 (21)	0.67± 0.22 (66)
RT	0.70± 0.29 (9)	0.82± 0.20 (4)	0.57± 0.24 (3)	0.70± 0.26 (16)
SB	0.57± 0.21 (24)	0.66± 0.18 (23)	0.66± 0.15 (23)	0.63± 0.19 (70)
TBIO	0.57± 0.23 (23)	0.69± 0.19 (19)	0.69± 0.17 (19)	0.65± 0.21 (61)
S/R	0.52± 0.13 (6)	0.28± 0.11 (4)	0.23± 0.17 (2)	0.39± 0.18 (13)
H/D	0.53± 0.17 (18)	0.45± 0.12 (11)	0.45± 0.14 (9)	0.49± 0.15 (38)

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[a] See table 1.1 for description of traits.

Table 2.11 Mean type B genetic correlation estimates and the standard deviations between 15-year field tree height and seedling traits of the same families observed under different nutrient (N) and water (W) treatment conditions in the greenhouse[a]

Seedling trait	Treatment Combinations					
	N1W1	N1W2	N1W3	N2W1	N2W2	N2W3
H0	0.49±0.10	0.60±0.20	0.48±0.22	0.33±0.30	0.45± (1)	0.35±0.15
H1	0.69±0.09	0.65±0.06	0.80±0.15	0.61±0.20	0.67±0.10	0.52±0.09
H2	0.67±0.09	0.65±0.05	0.78±0.10	0.61±0.17	0.66±0.13	0.52±0.08
H3	0.72±0.07	0.66±0.05	0.81±0.07	0.69±0.10	0.69±0.15	0.66±0.10
H4	0.74±0.07	0.63±0.06	0.81±0.07	0.70±0.09	0.72±0.15	0.65±0.08
NH1-0	0.69±0.10	0.68±0.04	0.86±0.12	0.72±0.16	0.67±0.09	0.59±0.05
NH2-0	0.61±0.08	0.65±0.03	0.81±0.06	0.65±0.13	0.62±0.13	0.54±0.07
NH3-0	0.68±0.06	0.65±0.10	0.82±0.09	0.74±0.10	0.67±0.16	0.69±0.11
NH4-0	0.70±0.06	0.61±0.11	0.84±0.07	0.75±0.11	0.70±0.16	0.67±0.09
NH3-2	0.86±0.11	0.56±0.27	0.68±0.27	0.68±0.16	0.64±0.18	0.84± (1)
NH4-2	0.86±0.08	0.47±0.29	0.95± (1)	0.68±0.21 (3)	0.51± (1)	0.84± (1)
D1	0.62±0.14 (3)	0.59±0.12	0.82±0.12	0.35±0.20	0.45±0.07 (3)	0.49±0.11 (3)
D2	0.67±0.12	—	0.82±0.10	0.46±0.20	0.49±0.08	0.55±0.06 (3)
D3	0.76±0.09	0.71±0.32 (2)	0.97±0.06 (3)	0.66±0.02 (3)	0.44±0.08	0.53±0.14
Ne	0.70±0.13	0.71±0.09	0.87±0.11	0.56±0.16	0.56±0.11	0.55±0.11
Ust	0.75±0.06	0.48±0.15	0.92±0.05		0.63±0.08	0.58±0.11 (3)
Lst	0.87±0.10	0.81±0.26 (2)	0.94±0.05	0.63±0.17	0.57±0.08	0.52±0.08 (3)
Rt	0.35± (1)	—	0.82± (1)	—	0.53± (1)	—
SB	0.72±0.11	0.66±0.10	0.88±0.09	0.57±0.14	0.52±0.10	0.62±0.07 (3)
Tbio	0.68±0.13	0.66±0.17 (3)	0.93±0.10	0.66±0.08 (3)	0.54±0.09	0.62± (1)
S/R	—	—	—	0.11 (1)	0.35 (1)	—
H/D average	0.48±0.05 (3)	0.24± (1)	—	0.46±0.18	—	0.53± (1)

Note: except those indicated by the number in brackets, all mean values and standard deviations were obtained based on 4 estimates.

[a] See table 1.1 for description of traits.

Table 2.12 **Spearman family rank correlations between greenhouse jack pine seedling traits and field tree height at plantation ages of 5, 10, and 15 years (number in brackets indicates the significant level)[a]**

Seedling Trait	Plantation ages (years)		
	5	10	15
H0	0.40 (0.05)	0.42 (0.04)	0.43 (0.03)
H1	0.56 (0.00)	0.64 (0.00)	0.66 (0.00)
H2	0.64 (0.00)	0.69 (0.00)	0.71 (0.00)
H3	0.65 (0.00)	0.71 (0.00)	0.72 (0.00)
H4	0.66 (0.00)	0.71 (0.00)	0.73 (0.00)
NH1-0	0.63 (0.00)	0.70 (0.00)	0.69 (0.00)
NH2-0	0.64 (0.00)	0.69 (0.00)	0.71 (0.00)
NH3-0	0.68 (0.00)	0.73 (0.00)	0.74 (0.00)
NH4-0	0.69 (0.00)	0.73 (0.00)	0.75 (0.00)
NH3-2	0.63 (0.00)	0.67 (0.00)	0.72 (0.00)
D1	0.43 (0.03)	0.50 (0.01)	0.51 (0.01)
D2	0.49 (0.01)	0.59 (0.00)	0.60 (0.00)
D3	0.52 (0.01)	0.63 (0.00)	0.61 (0.00)
Ne	0.61 (0.00)	0.70 (0.00)	0.70 (0.00)
Ust	0.59 (0.00)	0.69 (0.00)	0.69 (0.00)
St	0.58 (0.00)	0.66 (0.00)	0.66 (0.00)
Rt	0.50 (0.01)	0.63 (0.00)	0.63 (0.00)
SB	0.55 (0.00)	0.67 (0.00)	0.65 (0.00)
Tbio	0.53 (0.01)	0.65 (0.00)	0.64 (0.00)
H/D	0.57 (0.00)	0.51 (0.01)	0.54 (0.01)

[a] See table 1.1 for description of traits.

Table 2.13 Spearman family rank correlations between jack pine seedling traits and 15-year field tree height at four sites*

Trait	Site 1	Site 2	Site 3	Site 4
H0	0.32 (0.12)	0.56 (0.00)	0.35 (0.09)	0.31 (0.13)
H1	0.57 (0.00)	0.60 (0.00)	0.58 (0.00)	0.50 (0.01)
H2	0.63 (0.00)	0.60 (0.00)	0.63 (0.00)	0.52 (0.01)
H3	0.69 (0.00)	0.58 (0.00)	0.65 (0.00)	0.54 (0.01)
H4	0.68 (0.00)	0.58 (0.00)	0.66 (0.00)	0.54 (0.01)
NH1-0	0.66 (0.00)	0.57 (0.00)	0.63 (0.00)	0.53 (0.01)
NH2-0	0.60 (0.00)	0.59 (0.00)	0.65 (0.00)	0.49 (0.01)
NH3-0	0.71 (0.00)	0.59 (0.00)	0.68 (0.00)	0.51 (0.01)
NH4-0	0.70 (0.00)	0.59 (0.00)	0.69 (0.00)	0.54 (0.01)
NH3-2	0.81 (0.00)	0.53 (0.01)	0.60 (0.00)	0.51 (0.01)
D1	0.40 (0.05)	0.41 (0.04)	0.46 (0.02)	0.43 (0.03)
D2	0.49 (0.01)	0.47 (0.02)	0.56 (0.00)	0.46 (0.02)
D3	0.50 (0.01)	0.46 (0.02)	0.59 (0.00)	0.49 (0.01)
NE	0.65 (0.00)	0.56 (0.00)	0.64 (0.00)	0.50 (0.01)
UST	0.59 (0.00)	0.53 (0.01)	0.64 (0.00)	0.53 (0.01)
ST	0.59 (0.00)	0.51 (0.01)	0.61 (0.00)	0.52 (0.01)
RT	0.56 (0.00)	0.48 (0.01)	0.59 (0.00)	0.48 (0.01)
SB	0.57 (0.00)	0.51 (0.01)	0.61 (0.00)	0.49 (0.01)
TBIO	0.58 (0.00)	0.50 (0.01)	0.60 (0.00)	0.47 (0.02)
H/D	0.59 (0.00)	0.49 (0.01)	0.43 (0.03)	0.33 (0.11)
Mean site tree height	529.24	418.76	534.64	355.60
Number of significant Spearman correlations	94/120	79/120	94/120	54/120

* See table 1.1 for description of traits.

Table 2.14 Spearman family rank correlations between jack pine seedling traits observed under different nutrient (N) and water (W) treatment conditions and 15-year field tree height growth in Saskatchewan (significant levels are in brackets)*

Seedling trait	Treatment Combinations					
	N1W1	N1W2	N1W3	N2W1	N2W2	N2W3
H0	0.35 (0.08)	0.40 (0.05)	0.40 (0.05)	0.30 (0.15)	0.38 (0.06)	0.33 (0.11)
H1	0.61 (0.00)	0.54 (0.01)	0.62 (0.00)	0.57 (0.00)	0.59 (0.00)	0.57 (0.00)
H2	0.64 (0.00)	0.57 (0.00)	0.74 (0.00)	0.63 (0.00)	0.56 (0.00)	0.57 (0.00)
H3	0.70 (0.00)	0.60 (0.00)	0.76 (0.00)	0.66 (0.00)	0.58 (0.00)	0.62 (0.00)
H4	0.70 (0.00)	0.58 (0.00)	0.77 (0.00)	0.64 (0.00)	0.60 (0.00)	0.61 (0.00)
NH1-0	0.64 (0.00)	0.57 (0.00)	0.72 (0.00)	0.65 (0.00)	0.60 (0.00)	0.58 (0.00)
NH2-0	0.62 (0.00)	0.55 (0.00)	0.76 (0.00)	0.61 (0.00)	0.55 (0.00)	0.55 (0.00)
NH3-0	0.66 (0.00)	0.63 (0.00)	0.77 (0.00)	0.64 (0.00)	0.57 (0.00)	0.62 (0.00)
NH4-0	0.69 (0.00)	0.54 (0.01)	0.78 (0.00)	0.64 (0.00)	0.61 (0.00)	0.61 (0.00)
NH3-2	0.70 (0.00)	0.54 (0.01)	0.58 (0.00)	0.56 (0.00)	0.51 (0.01)	0.63 (0.00)
D1	0.51 (0.01)	0.48 (0.02)	0.60 (0.00)	0.26 (0.22)	0.28 (0.17)	0.44 (0.03)
D2	0.58 (0.00)	0.48 (0.02)	0.64 (0.00)	0.39 (0.05)	0.38 (0.06)	0.50 (0.01)
D3	0.63 (0.00)	0.37 (0.07)	0.77 (0.00)	0.45 (0.02)	0.30 (0.15)	0.52 (0.01)
Ne	0.63 (0.00)	0.66 (0.00)	0.81 (0.00)	0.50 (0.01)	0.44 (0.03)	0.57 (0.00)
Ust	0.63 (0.00)	0.43 (0.03)	0.79 (0.00)	0.57 (0.00)	0.47 (0.02)	0.51 (0.01)
St	0.72 (0.00)	0.52 (0.01)	0.81 (0.00)	0.56 (0.00)	0.47 (0.02)	0.48 (0.02)
Rt	0.44 (0.03)	0.44 (0.03)	0.78 (0.00)	0.40 (0.05)	0.43 (0.03)	0.51 (0.01)
SB	0.64 (0.00)	0.67 (0.00)	0.79 (0.00)	0.49 (0.01)	0.43 (0.03)	0.54 (0.01)
Tbio	0.57 (0.00)	0.60 (0.00)	0.81 (0.00)	0.45 (0.02)	0.41 (0.04)	0.51 (0.01)
H/D	0.33 (0.11)	0.47 (0.02)	0.32 (0.12)	0.54 (0.01)	0.43 (0.03)	0.26 (0.21)

Note: All mean values and standard deviations were calculated among the 4 field sites

* See table 1.1 for description of traits and table 1.2 for description of treatments.

Table 2.15 Mean percent of correct identification of 15-year field family classes with 20 greenhouse seedling traits observed under different nutrient (N) and water (W) conditions[a]

Field site	Family class	N1			N2			
	(field)	W1	W2	W3	W1	W2	W3	Mean
1	1	63.75	58.75	68.75	56.25	57.50	65.63	61.77
	2	38.33	41.11	52.78	31.11	32.78	31.11	37.87
	3	58.48	66.25	67.77	41.07	54.73	40.71	54.84
	Mean	53.52	55.37	63.10	42.81	48.34	45.82	51.49
2	1	53.13	47.50	60.00	46.88	50.00	56.25	52.29
	2	55.00	41.67	52.22	51.67	36.67	50.56	47.96
	3	64.29	62.77	73.57	55.09	55.09	53.21	60.67
	Mean	57.47	50.64	61.93	51.21	47.25	53.34	53.64
3	1	56.25	50.00	60.00	46.88	53.75	61.88	54.79
	2	38.89	35.56	37.78	45.00	39.44	43.33	40.00
	3	56.16	49.38	54.46	65.09	51.79	47.32	54.03
	Mean	50.43	44.98	50.75	52.32	48.33	50.84	49.61
4	1	55.63	51.88	57.50	51.88	44.38	53.13	52.40
	2	45.56	47.22	45.56	43.89	41.67	42.78	44.44
	3	50.00	63.93	55.98	46.79	53.04	39.11	51.47
	Mean	50.39	54.34	53.01	47.52	46.36	45.00	49.44
Across 4 field sites	1	57.19	52.03	61.56	50.47	51.41	59.22	55.31
	2	44.44	41.39	47.08	42.92	37.64	41.94	42.57
	3	57.23	60.58	62.95	52.01	53.66	45.09	55.25
Mean		52.95	51.33	57.20	48.46	47.57	48.75	51.05
		53.83			48.26			

Note: family classes 1, 2 and 3 refer to the fast-, average- and slow-growing field family classes respectively.

[a] See table 1.2 for description of greenhouse treatments on jack pine seedlings.

Table 2.16 Percents and standard deviations of correctly identifying the fast-growing field family class with different seedling traits (based on the mean of 6 treatment combinations) at 4 filed sites[a]

Trait	Site 1 (%)	Site 2 (%)	Site 3 (%)	Site 4 (%)	combined (%)
H0	31.25 ± 10.5	43.85 ± 10.5	37.50 ± 13.7	35.42 ± 12.3	37.00 ± 11.9
H1	56.25 ± 6.8	58.33 ± 6.5	56.25 ± 6.8	50.00 ± 7.9	55.21 ± 7.3
H2	64.58 ± 5.1	56.25 ± 6.8	56.25 ± 6.8	60.42 ± 5.1	59.38 ± 6.6
H3	68.75 ± 10.5	56.25 ± 10.5	60.41 ± 5.1	56.25 ± 10.5	60.47 ± 10.2
H4	68.75 ± 6.8	56.25 ± 6.8	58.33 ± 6.5	58.33 ± 10.2	60.42 ± 8.8
NH1-0	64.58 ± 5.1	58.33 ± 6.4	60.41 ± 9.4	54.17 ± 6.4	59.37 ± 7.6
NH2-0	68.75 ± 13.1	52.08 ± 9.4	54.17 ± 6.5	52.08 ± 9.4	56.77 ± 11.6
NH3-0	70.83 ± 10.2	56.25 ± 6.8	58.33 ± 6.5	54.17 ± 10.2	59.90 ± 10.4
NH4-0	75.00 ± 7.9	58.33 ± 10.2	60.42 ± 12.3	56.25 ± 6.8	62.50 ± 11.7
NH3-2	62.50 ± 11.2	54.17 ± 15.1	62.50 ± 15.8	54.17 ± 10.2	58.33 ± 13.1
D1	47.92 ± 5.1	45.83 ± 6.5	43.75 ± 6.8	52.08 ± 9.4	47.40 ± 7.3
D2	54.17 ± 12.9	43.75 ± 10.5	47.92 ± 12.3	52.08 ± 12.3	49.48 ± 11.9
D3	58.33 ± 12.9	50.00 ± 7.9	52.08 ± 12.3	52.08 ± 9.4	53.13 ± 10.6
NE	62.50 ± 11.2	50.00 ± 11.2	58.33 ± 17.1	52.08 ± 5.1	55.73 ± 12.2
UST	70.83 ± 12.9	54.17 ± 15.1	58.33 ± 17.1	54.17 ± 17.1	59.38 ± 16.2
LST	68.75 ± 10.5	54.17 ± 10.2	56.25 ± 13.1	56.25 ± 10.5	58.58 ± 11.9
RT	56.25 ± 10.5	45.83 ± 10.2	50.00 ± 13.7	50.00 ± 7.9	50.52 ± 10.7
SB	64.58 ± 5.4	52.08 ± 9.4	60.42 ± 14.6	52.08 ± 5.1	57.29 ± 11.0
TBIO	62.50 ± 7.9	50.00 ± 7.9	54.17 ± 10.2	54.17 ± 6.5	55.21 ± 9.0
H/D	58.33 ± 10.2	50.00 ± 7.9	50.00 ± 11.2	41.67 ± 6.5	50.00 ± 10.4
Average	61.77 ± 13.2	52.29 ± 9.0	54.79 ± 12.3	52.39 ± 10.0	55.31 ± 11.4

[a] See table 1.1 for description of traits.

Table 2.17 Percents and standard deviations of correct identification of the slow-growing 15-year filed family class with different seedling traits (based on the mean of 6 treatment combinations) at 4 filed sites[a]

Trait	Site 1 (%)	Site 2 (%)	Site 3 (%)	Site 4 (%)	combined (%)
H0	52.68 ± 13.7	66.07 ± 5.6	50.00 ± 7.9	43.45 ± 9.7	53.05 ± 12.3
H1	60.71 ± 15.5	63.99 ± 11.8	56.25 ± 13.4	47.62 ± 14.8	57.14 ± 14.4
H2	58.33 ± 17.3	66.37 ± 8.5	58.33 ± 11.2	58.93 ± 8.3	60.49 ± 11.6
H3	63.39 ± 17.6	70.24 ± 6.2	56.55 ± 5.6	60.71 ± 12.3	62.72 ± 11.9
H4	58.04 ± 16.5	69.64 ± 5.8	56.55 ± 5.6	56.55 ± 10.6	60.19 ± 11.4
NH1-0	56.55 ± 19.2	62.50 ± 11.2	58.33 ± 13.4	49.70 ± 15.4	56.77 ± 14.9
NH2-0	54.76 ± 16.2	65.18 ± 10.3	58.63 ± 9.3	57.74 ± 10.1	59.08 ± 11.7
NH3-0	59.82 ± 16.7	69.64 ± 5.8	56.55 ± 5.6	58.33 ± 11.2	61.08 ± 11.3
NH4-0	59.23 ± 16.1	65.77 ± 7.9	54.46 ± 5.3	56.55 ± 11.6	59.00 ± 11.1
NH3-2	62.80 ± 11.1	51.79 ± 8.9	43.75 ± 13.9	50.60 ± 12.4	52.23 ± 13.0
D1	43.75 ± 15.3	50.89 ± 15.1	45.54 ± 5.3	41.67 ± 6.5	45.46 ± 11.3
D2	48.81 ± 16.1	53.87 ± 12.6	51.19 ± 8.4	45.54 ± 13.1	49.85 ± 12.4
D3	45.54 ± 13.1	55.95 ± 17.0	51.79 ± 20.1	44.64 ± 12.8	49.47 ± 15.7
NE	53.27 ± 13.2	58.63 ± 13.0	52.98 ± 13.7	50.89 ± 13.6	53.94 ± 12.8
UST	51.49 ± 11.9	56.25 ± 11.4	58.63 ± 9.3	54.17 ± 9.1	55.13 ± 10.1
ST	50.00 ± 12.1	58.33 ± 11.2	57.74 ± 9.2	50.89 ± 7.8	54.24 ± 10.3
RT	55.36 ± 11.8	58.04 ± 15.1	56.25 ± 13.1	46.13 ± 12.1	53.94 ± 13.1
SB	53.27 ± 13.2	61.90 ± 15.3	52.98 ± 13.7	53.27 ± 12.4	55.35 ± 13.3
TBIO	55.95 ± 12.9	61.31 ± 15.4	56.25 ± 11.4	52.08 ± 13.9	56.40 ± 13.0
H/D	52.98 ± 11.2	47.02 ± 17.6	47.92 ± 16.5	50.00 ± 4.5	49.48 ± 12.8
Average	54.84 ± 14.4	60.67 ± 12.7	54.03 ± 11.3	51.47 ± 11.8	55.25 ± 12.6

[a] See table 1.1 for description of traits.

Table 2.18 Percents and standard deviations in correctly identifying the 15-year fast-growing family class with seedling traits observed under different nutrient (N) and water (W) conditions[a]

Seedling trait	Treatment Combination					
	N1W1 (%)	N1W2 (%)	N1W3 (%)	N2W1 (%)	N2W2 (%)	N2W3 (%)
H0	31.3±7.2	56.3±7.2	43.8±7.2	28.1±6.3	31.3±7.2	31.3±7.2
H1	56.3±7.2	56.3±7.2	53.1±6.3	56.3±7.2	46.9±6.3	62.5±0.0
H2	56.3±7.2	62.5±0.0	62.5±0.0	56.3±7.2	53.1±6.3	65.6±6.3
H3	65.6±6.3	56.3±7.2	65.6±6.3	65.6±6.3	47.8±7.2	65.6±6.3
H4	65.6±6.3	56.3±7.2	65.6±6.3	56.3±7.2	53.1±12.0	65.6±6.3
NH1-0	56.3±7.2	56.3±7.2	56.3±7.2	65.6±6.3	56.3±7.2	65.6±6.3
NH2-0	43.8±7.2	56.3±7.2	65.6±15.7	65.6±6.3	56.3±12.5	53.1±6.3
NH3-0	53.2±12.0	56.3±7.2	65.6±15.7	65.6±6.3	53.1±6.3	65.6±6.3
NH4-0	68.8±7.2	46.9±12.0	65.6±15.7	65.6±6.3	62.5±10.2	65.6±6.3
NH3-2	68.8±7.2	37.5±10.2	62.5±0.0	50.0±0.0	62.5±10.2	68.8±7.2
D1	43.8±7.2	53.1±6.3	53.1±6.3	43.8±7.2	40.6±6.3	50.0±0.0
D2	56.3±7.2	56.3±7.2	56.3±7.2	31.3±7.2	40.6±6.3	56.3±7.2
D3	53.1±6.3	43.8±7.2	56.3±7.2	56.3±7.2	43.8±7.2	65.6±12.0
Ne	68.8±7.2	43.8±7.2	65.6±12.0	43.8±7.2	56.3±7.2	56.3±7.2
Ust	68.8±7.2	43.8±12.5	78.1±6.3	43.8±7.2	56.3±16.1	65.6±12.0
Lst	68.8±7.2	53.1±6.3	65.6±6.3	43.8±7.2	56.3±12.5	65.6±12.0
Rt	46.9±12.0	40.6±6.3	62.5±0.0	40.6±6.3	56.3±7.2	56.3±7.2
SB	68.8±7.2	53.1±6.3	65.6±12.0	43.8±7.2	56.3±7.2	56.3±7.2
Tbio	56.3±7.2	53.1±6.3	65.6±6.3	43.8±7.2	56.3±7.2	56.3±7.2
H/D	46.9±6.3	59.4±15.7	56.3±7.2	43.8±12.5	46.9±6.3	46.9±6.3
Average	57.2±12.5	52.0±9.8	61.6±10.5	50.5±13.0	51.4±11.1	59.2±11.0

Note: All mean values and standard deviations were calculated among the 4 field sites.

[a] See table 1.1 for description of traits and table 1.2 for description of nutrient (N) and water (W) treatments.

Table 2.19 Percents and standard deviations in correctly identifying the 15-year slow-growing family class with seedling traits observed under different nutrient (N) and water (W) conditions[a]

Seedling trait	Treatment Combination					
	N1W1 (%)	N1W2 (%)	N1W3 (%)	N2W1 (%)	N2W2 (%)	N2W3 (%)
H0	53.1±12.0	58.5±10.5	50.0±10.2	43.8±16.1	59.8±15.8	53.1±8.5
H1	68.8±7.9	50.0±5.8	70.5±15.0	56.7±12.7	57.1±11.7	39.7±9.0
H2	66.5±8.2	69.2±4.5	65.6±12.0	56.3±16.2	58.5±2.7	46.9±8.5
H3	65.6±6.3	70.5±8.9	70.5±15.0	52.7±11.3	65.6±7.0	51.3±8.2
H4	59.4±12.0	67.9±7.1	65.6±12.0	52.7±11.3	65.6±7.0	50.0±10.2
NH1-0	71.0±5.9	50.0±5.8	70.5±15.0	56.3±16.1	53.1±8.5	39.7±9.0
NH2-0	62.9±8.4	67.9±7.1	67.4±9.0	56.3±16.1	53.1±6.3	46.9±8.5
NH3-0	60.7±7.1	71.9±6.3	65.6±12.0	52.7±11.3	65.6±7.0	50.0±10.2
NH4-0	56.7±5.1	67.9±7.1	65.6±12.0	51.3±10.0	65.6±7.0	46.9±8.5
NH3-2	56.3±16.1	52.2±20.2	53.1±12.0	53.1±8.5	59.4±6.3	39.3±7.1
D1	50.0±10.2	46.9±6.3	59.4±12.0	35.7±7.6	37.5±10.2	43.3±5.1
D2	50.0±10.2	56.3±12.5	59.4±12.0	43.8±16.1	50.0±8.2	39.7±9.0
D3	50.0±10.2	44.2±21.6	65.6±15.7	46.4±18.0	50.0±10.2	40.6±12.0
Ne	54.9±6.1	66.1±15.6	62.5±15.6	53.1±8.5	43.3±5.1	43.8±7.2
Ust	54.9±8.4	53.1±8.5	63.4±11.8	56.3±13.4	56.3±7.21	46.9±8.5
Lst	53.1±8.5	61.2±2.7	61.2±10.6	53.1±15.7	50.0±8.2	46.9±8.5
Rt	53.1±8.5	64.7±4.5	66.5±18.4	53.1±8.5	43.3±5.1	42.9±10.1
SB	54.9±6.1	66.1±15.6	69.2±14.8	50.0±10.2	46.9±6.3	45.1±6.1
Tbio	53.1±8.5	70.5±8.9	66.5±18.4	53.1±8.5	50.0±5.8	45.1±6.1
H/D	49.6±9.3	56.7±5.1	40.6±12.0	63.8±10.1	42.4±16.8	43.8±7.2
Average	57.2±10.2	60.6±12.6	62.9±13.9	52.0±12.6	53.7±11.4	45.1±8.4

Note: All mean values and standard deviations were calculated among the 4 field sites.

[a] See table 1.1 for description of seedling traits and table 1.2 for description of greenhouse treatments.

Table 2.20 Percent of serious mis-identification the fast- and slow-growing family classes with seedling traits observed under different nutrient (N) and water (W) conditions[a]

Seedling trait	Treatment Combinations					
	N1W1 (%)	N1W2 (%)	N1W3 (%)	N2W1 (%)	N2W2 (%)	N2W3 (%)
H0	6.0 ± 2.1	6.0 ± 2.1	5.5 ± 2.1	6.0 ± 2.1	5.5 ± 2.1	5.0 ± 1.9
H1	3.0 ± 2.8	4.0 ± 3.0	3.5 ± 2.6	4.0 ± 3.0	4.0 ± 2.1	6.0 ± 2.1
H2	5.0 ± 1.9	5.5 ± 2.1	4.5 ± 1.4	4.0 ± 3.0	5.5 ± 2.1	5.0 ± 2.8
H3	5.5 ± 2.1	5.0 ± 1.9	4.5 ± 1.4	3.0 ± 2.8	5.5 ± 2.1	4.5 ± 3.3
H4	3.0 ± 2.8	5.5 ± 2.1	5.0 ± 1.9	3.0 ± 2.8	5.5 ± 2.1	4.5 ± 3.3
NH1-0	3.0 ± 2.8	3.0 ± 2.8	2.5 ± 3.0	5.0 ± 2.8	4.0 ± 2.1	6.0 ± 2.1
NH2-0	5.0 ± 1.9	5.5 ± 2.1	4.5 ± 1.4	3.0 ± 2.8	5.5 ± 2.1	5.0 ± 2.8
NH3-0	5.5 ± 2.1	5.5 ± 2.1	4.5 ± 1.4	3.0 ± 2.8	5.5 ± 2.1	4.5 ± 3.3
NH4-0	2.5 ± 3.0	5.5 ± 2.1	4.5 ± 1.4	3.0 ± 2.8	5.5 ± 2.1	4.5 ± 3.3
NH3-2	5.5 ± 2.1	4.5 ± 2.6	5.0 ± 1.9	5.0 ± 2.8	4.5 ± 3.3	4.5 ± 3.3
D1	5.0 ± 1.9	4.0 ± 3.0	4.5 ± 1.4	5.0 ± 2.8	6.0 ± 2.1	6.0 ± 2.1
D2	5.5 ± 2.1	3.0 ± 2.8	4.5 ± 1.4	5.0 ± 2.8	5.5 ± 2.1	6.0 ± 2.1
D3	5.0 ± 1.9	5.0 ± 2.8	4.5 ± 1.4	6.0 ± 2.1	5.0 ± 1.9	3.0 ± 2.8
Ne	5.5 ± 2.1	4.5 ± 1.4	5.0 ± 1.9	6.0 ± 2.1	5.5 ± 2.1	5.0 ± 2.8
Ust	4.0 ± 3.0	5.0 ± 2.8	1.5 ± 2.1	5.0 ± 2.8	5.5 ± 2.1	3.0 ± 2.8
Lst	3.0 ± 2.8	4.0 ± 3.0	4.5 ± 1.4	5.0 ± 2.8	5.5 ± 2.1	3.0 ± 2.8
Rt	5.5 ± 2.1	5.5 ± 2.1	5.0 ± 1.9	5.0 ± 2.8	6.0 ± 2.1	5.0 ± 2.8
SB	5.5 ± 2.1	4.5 ± 1.4	5.0 ± 1.9	6.0 ± 2.1	5.5 ± 2.1	6.0 ± 2.1
Tbio	5.5 ± 2.1	5.0 ± 1.9	5.0 ± 1.9	5.0 ± 2.8	5.5 ± 2.1	5.0 ± 2.8
H/D	5.0 ± 2.8	4.5 ± 2.6	6.0 ± 2.1	5.0 ± 2.8	4.5 ± 2.6	6.0 ± 2.1

Note: All mean values and standard deviations were calculated among the 4 field sites.

[a] See table 1.1 for description of seedling traits and table 1.2 for description of greenhouse nutrient (N) and water (W) treatments.

Table 2.21 Relative selection efficiency (RSE) of selecting jack pine family at 1-year seedling age (comparing with family selecting at plantation age of 15 years)*

Seedling Trait	Seedling h_f^2	Type B r_g	15-year h_f^2	RSE
H0	0.90	0.45	0.82	1.41
H1	0.94	0.59	0.82	1.90
H2	0.90	0.65	0.82	2.04
H3	0.89	0.70	0.82	2.19
H4	0.90	0.71	0.82	2.23
NH2-0	0.88	0.65	0.82	2.02
NH3-0	0.88	0.71	0.82	2.21
NH4-0	0.89	0.71	0.82	2.22
NH3-2	0.84	0.69	0.82	2.10
NH4-2	0.86	0.69	0.82	2.12
D1	0.85	0.56	0.82	1.71
D2	0.80	0.60	0.82	1.78
D3	0.76	0.66	0.82	1.91
Ne	0.69	0.66	0.82	1.82
Ust	0.62	0.68	0.82	1.77
St	0.69	0.72	0.82	1.98
Rt	0.77	0.57	0.82	1.66
SB	0.61	0.66	0.82	1.71
Tbio	0.68	0.69	0.82	1.89

Note: additional 5 and 3 years are added for breeding with one-year seedling and 15-year plantation tree respectively.

* h_f^2 is the family heritability estimate and r_g is the type B genetic correlation estimate between greenhouse seedling trait and 15-year field tree height respectively.

CHAPTER 3 GENERAL SUMMARY AND DISCUSSION

The long time required for evaluating breeding values of a forest tree at its mature age has been a major obstacle for increasing the breeding efficiency in temperate conifer tree improvement programs (Wu 1993). Early selection was proposed, theoretically, as an effective way to substantially shorten the breeding cycle, aiming to achieve more genetic gain per unit time (Lambeth 1980). However, for a successful indirect early selection, available early traits that are highly heritable and give reliable prediction of mature performance are crucial (Lambeth 1980, Jiang 1985). Although high heritability can often be obtained in early traits through more uniform early testing environments and efficient experimental design (Smith 1992; Wu 1993), weak early-mature genetic correlation remains a major restraint for the practical application of early selection (Eriksson 1993). For decades, extensive early test studies have resulted in inconclusive results as what the strength of early-mature genetic correlations are and what kind of early test nutrient and water conditions should be adopted to achieve higher early-mature genetic correlations (Cannell et al. 1978; Li et al. 1992; Eriksson et al. 1993).

In this study, varying nutrient and water treatment levels were employed in the greenhouse to study their effects on seedling growth of 25 open-pollinated jack pine families and their effects on the greenhouse-field correlations. Genetic variation, family stability and family-by-treatment (or genotype-by-environment) interaction were evaluated under greenhouse and field conditions. The predictability of seedling traits to 5- 10- and 15-year field height were compared under different greenhouse treatment conditions with three evaluating indicators (i.e. the type B genetic correlation, Spearman family rank correlation and the percent of correct identification of field family classes).

3.1 Summary of the results

Results of this thesis were mainly presented in the following aspects:

1. The effects of nutrient treatment were highly significant ($P<0.001$) for all seedling traits observed (i.e. height, height increment, basal diameter, diameter increment, growth period, organ dry biomass and biomass allocation) except for H/D ratio. The effects of water treatment were significant on all greenhouse traits at the probability level of 0.05 except seedling height. Favourable growth conditions, e.g. high nutrient supply (200 ppm) and frequent watering (water interval < 1 week) resulted in a longer growth period, larger seedling size and higher shoot/root ratio. Despite their significant individual effects, nutrient x water interaction was negligible on most seedling traits.

2. The effect of seed weight on seedling growth was significant throughout the greenhouse study. Families with heavier seed weight generally yielded larger seedling size. The effect of seed weight was stronger at the high nutrient level (200 ppm) than at the low nutrient level (20 ppm), but did not differ significantly among the three water treatment levels. Although family seed weight was not significantly correlated to 15-year family mean height in the field, it was found that the fast-

growing families generally had heavier seed weights relative to the slow-growing families. Correlations studies before and after seed weight adjustment indicated that seed weight adjustment is not recommended for early genetic evaluation in jack pine because the correlations between seedling traits and 15-year field tree height of the same families were higher before seed weight adjustment than after seed weight adjustment.

3. Genetic variation among the 25 open-pollinated jack pine families was highly significant for all seedling traits except for S/R (shoot/root) ratio. Genetic differences among family classes were greater than among families within family classes. Family class x treatment (either nutrient or/and water) interactions were not significant for all seedling traits. Although families/family class x nutrient treatment interaction was significant at the 0.05 probability level for several seedling traits, families/family class x water treatment and families/family class x nutrient x water treatment interactions were not significant for almost all traits. The high type B genetic correlation and family rank correlation between seedlings growing in the two nutrient levels indicated the stable performance of open-pollinated jack pine families under varying nutrient and water treatments.

High heritability estimates were obtained with seedling traits. Family heritability was highest for seedling height (0.80 - 0.94), followed by height increment (0.50 - 0.96), basal diameter (0.67 - 0.85) and organ dry biomass (0.50 - 0.77). However, For shoot/root ratio (S/R), family heritability estimates were only about 0.2.

4. In the field, genetic differences among family were highly significant over time. Family variance components accounted for 18.54 % of the total phenotypic variation in height at age 15. Family x replication interaction was significant for all field growth traits over plantation ages. However, family x site interaction was insignificant and accounted for less than 3% of total phenotypic variance, despite the fact that there was large difference among sites in site-quality as indicated by averaged growth of trees. Estimates of family heritability for 15-year tree height and diameter were high, ranging from 0.58 to 0.74 for height and from 0.48 to 0.70 for diameter respectively. This high heritability might be inflated by sampling methods used in this study.

5. High greenhouse-field correlations ($r>0.60$) and good prediction of field growth (55% of correct identification of superior or inferior field family classes) were obtained between seedling traits and 15-year field tree height growth under all greenhouse treatment conditions and 4 field sites. This indicated that early selection is promising in jack pine. Such results were consistent with the relatively weak G x E interactions in the greenhouse and in the field.

Seedling height, height increment and organ dry biomass yielded higher average genetic correlation (0.57 - 0.71) with 15-year field height than other seedling growth traits. The percentage of correct identification of 15-year field family classes with 20 different seedling trait averaged 55% for the fast- and slow-growing field family classes and 43% for the average-growing field family class. Despite the fact that there were frequent mis-classification between the fast- and average-growing or the slow- and average-growing field family classes, the percent for mis-classification between the fast- and slow-growing classes was under 8% for any of those 20 seedling traits. Contrastingly, shoot/root ratio and the length of growth period were not discriminative to field family classes, indicating their poor predictability in jack pine, although this trait has been shown as the best early predictor in lodgepole pine (Wu, 1993) and a good predictor in loblolly pine (Waxler and van Bujitenen 1981).

6. Comparatively low nutrient condition, especially the treatment combination of low nutrient and frequent water (N1W3), in the greenhouse yielded persistently higher greenhouse-field correlation or better prediction of 15-year field growth. This could be the result of sampling error and/or seedling competition at the high nutrient level. It could also be the result of mimicking field nutrient conditions in Saskatchewan, where jack pine tests were established on sand or sandy soil and where nutrient deficiency is likely to be a major limiting factor for tree growth.

3.2 Discussion

Chapter 1 of this thesis was the first investigation dealing with the genetic response among jack pine seedlings to the joint effect of nutrient and water treatments. Information inferred from this study could be useful in understanding the strength of GE interactions with varying nutrient and water conditions in the seedling stage. The results indicated that although nutrient x family interaction was significant, its variance component seldom exceeded 3% of total phenotypic variance in most seedling traits and was only one-fourth to one-tenth of family variance. Thus, the relative strength of nutrient x family interaction was not strong. Similarly, insignificant G x E interaction was observed in the field (chapter 2 of this thesis). This was consistent with previous reports (Greenwood and Volkaert 1992) that G x E interaction is generally weak in jack pine. The weak G x E interaction resulted in the stable family performance and high family rank correlation across greenhouse treatment levels and field sites. Influence of weak G x E interaction to tree improvement in jack pine could be significant since a base breeding population could basically be able to satisfy the breeding requirements for different field conditions within a breeding zone. Consequently the breeding efficiency, in terms of genetic gain per unite investment, could be greatly improved. The weak G x E interaction might also be responsible for the generally high greenhouse-field correlations obtained in this study under different greenhouse treatment levels and field conditions, although there were some small differences in scale. In addition, weak G x E interaction in jack pine appeared to be common cross the range of the species and did not differ greatly between the eastern and northwestern populations (Adams and Morgenstern 1991; Greenwood and Volkaert 1992). Thus, it could be the reason that consistently good prediction of later field growth with early trait were obtained among studies using different population and different early testing conditions (Magnussen and Yeatman 1986; Riemenschneider 1988; Carter et al. 1990). However, since the sample of this study included many top- and bottom-ranking families, the treatment x family interaction could be under estimated and family variation, heritability and stability might be inflated. Therefore, to confirm the weak GE interaction in jack pine seedling and in field tree in Saskatchewan, a larger and complete random sample of families would be needed.

In agreement with previous studies (William 1987; Cater et al. 1990; Li et al. 1992), seedling height growth gave persistently better prediction of field growth than other seedling traits. In this study, seedling absolute height or height growth increment beyond the hypocotyl not only had the highest family and individual heritability estimates, but also yielded the highest genetic correlation (0.64-0.70) with 15-year field height. Therefore, there is no doubt that they should be the target seedling traits for early selection in jack pine. Other seedling traits, though they also gave good prediction of 15-year field growth, are inferior to seedling height and height increment because of their relatively low heritability estimates and greenhouse-field correlations. The insignificant correlation between LGP (or S/R) and growth may provide the possibility for spontaneously improving seedlings adaptability and the growth rate.

The high greenhouse-field genetic correlation in the first growing season implied that a large number of jack pine families could be screened in the greenhouse with seedling height. Consequently, it could be an effective approach to cull the poor performing families in conjunction with operational nursery seedling production. For tree breeding programs, the high greenhouse-field correlation in the first growing season could imply that a large number of families can be precisely tested under uniform greenhouse conditions in a relatively short time. In doing so, the family selection intensity could be greatly increased. However, due to the sampling method used in this study, greenhouse-field genetic correlation might have been inflated, and further corroboration of the result would be needed.

Despite the consistence with previous reports that high early-mature correlation exists in jack pine (Magnussen and Yeatman 1986; Riemenschneider 1988; Carter et al. 1990), results in this study also indicated that nutrient stressed early testing conditions could improve the prediction of field performance. This is not in contradiction to the weak G x E interaction detected. Although the strength of G x E interaction was relatively weak, its effect was still significant. Therefore, it was able to affect family ranking to some extent, resulting in the difference in early-mature correlation. It is worthwhile to notice that the growth medium (1:1:1 mixture of sand, peat moss and vermiculate (volume)) used in this study might also have contributed to the high greenhouse-field correlations since the rather sandy growth medium was similar to the actual field soil conditions. Compared with another crop of the same families using pure peat moss as the growth medium, seedling height in this study was relatively small (55 vs 110 cm at age of two months), but it had higher correlation with field growth (0.71 vs 0.64 in Spearman family rank correlation). Therefore, evidence in this study appeared to support the hypothesis that early-mature correlation of jack pine in Saskatchewan could be improved by mimicking tree growing conditions in the field. To confirm this finding, further investigation on the best early testing nutrient and soil conditions would needs to be conducted.

Almost all early genetic evaluation studies have been based on the genetic correlation between early trait(s) and mature growth such as mature height or stem volume. This direct connection with the ultimate breeding goal of volume improvement may not always be able to achieve the best economic benefits. It could be possible that wood quality will decrease with the increased growth rate. For example, height growth was found to be unfavourably correlated with stem crook in jack pine (Morris 1991). Therefore, maximum increase in height growth will result in a trade-off in terms of number of stem crooks. Studies on the genetic correlation between early trait(s) and mature selection index could be a more appropriate approach than with single mature growth trait(s). This is because mature selection index is usually the best compromise between favourable and unfavourable genetic gain, thus, representing the highest economic benefit of breeding.

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